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Predicting Encounter Rates for Zooplankton: A Model Assuming a Cylindrical Encounter Field

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GIGUÈRE, L. A., A. DELÀGE, L. M. DILL, AND J. GERRITSEN. 1982. Predicting encounter rates for zooplankton: a model assuming a cylindrical encounter field. Can. J. Fish. Aquat. Sci. 39: 237 – 242.

We delimit a cylindrical attack field for a *Chaoborus* larva feeding on zooplankton, and propose a mathematical model to predict encounter rates with prey for this ambush predator. The model is based on the encounter process between a stationary cylinder and spheres moving at constant velocity in random directions. The predictions of the model are corroborated in the laboratory.

Key words: zooplankton, encounter model, *Chaoborus*, ambush predator, copepod

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Nous délimitons un champ d'attaque cylindrique chez une larve de *Chaoborus* qui se nourrit de zooplancton, et nous proposons un modèle mathématique qui prédit le taux de rencontre avec des proies pour ce prédateur à l'affût. Le modèle se base sur le processus de rencontre d'un cylindre stationnaire avec des sphères qui se déplacent au hasard et à vitesse constante. Les prédictions du modèle sont supportées par des observations recueillies en laboratoire.

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IN coastal lakes and ponds near Vancouver, British Columbia, the 4th instar larva of *Chaoborus trivittatus* feeds primarily on crustacean zooplankton (mainly copepods, Fedorenko 1975; Swift 1976; Giguère 1979); larvae hover in the water and strike at prey that approach closely (≤3.8 mm, Giguère and Dill 1979). Because (a) larvae do not pursue or lunge at prey, (b) prey move in more or less unpredictable directions, (c) predator and prey live in a relatively uniform aquatic environment, stochastic collision models could be used to quantify this encounter process accurately. To do so, one must imagine a suitable patch in space within which prey are uniformly or randomly distributed and move in random directions. Prey will encounter a target volume (the ambush predator) according to a function that depends on the size and speed of the prey, and the size and shape of the strike field of the predator.

The objectives of this paper are therefore threefold: first, to delimit the effective strike field of a *Chaoborus* larva; second, propose a mathematical formulation describing the rate at which prey encounter this strike field; and third, to demonstrate the ability of this model to make accurate quantitative predictions by comparing its output to encounter data collected in the laboratory, using copepods as prey.

Materials and Methods

The configuration of the strike field of a starved 4th instar larva of *Chaoborus* was determined by filming predator–prey interactions at 45–150 frames/s with a Ciné-8 camera (Visual Instrumentation Corp., Burbank, Calif.). Larvae averaging 14.8 mm long (SE = 0.95, based on sample measurement) were starved for at least 1 day, and offered copepod prey (*Diaptomus kenai* and *D. leptopus*, 0.9–2.6 mm in length) at 6, 13, and 24°C.

The filming was done from above a small Plexiglas container with about 6–8 mL of lake water. The shortest distance between the prey and the center of the predator at the moment of attack was measured on film perpendicular to the main body axis of the predator (left and right sides were pooled). Because these measurements are of a projection of the position of the prey onto the two-dimensional horizontal plane through the predator, they underestimate true attack distances and are referred to as apparent attack distances.

To test the model predictions, copepods were presented to single *Chaoborus* larvae inside rectangular experimental arenas containing 75 mL of lake water. Predator–prey interactions were observed visually and noted down as a time series with the help of an event recorder. An 'encounter' was scored whenever a part of the body of the prey (excluding antennae) came within 2 mm of the surface of the body of the predator. This included 93% of all attacks observed on high-speed films of predator–prey interactions (see Results below). Note that an encounter is not defined with respect to the sensory apparatus of the predator, but rather with respect to a volume of space within which prey become vulnerable to attack (whether or not prey detection occurred). This definition is simple (a sort of rule of thumb) and easily ascertained with the help of a millimetre grid applied to the bottom of Plexiglas containers. As deciding on an encounter involved judgment on the part of the observer, an initial training period of 33 h was needed until consistent observations were obtained.

Prey were divided visually into four approximate size (length) categories (I, 1.0–1.29 mm; II, 1.3–1.59 mm; III, 1.6–1.89 mm; IV, 2.0–2.29 mm). All prey size categories were presented at two densities (three and six prey/arena) at 13 and 24°C (unless otherwise indicated). The experiments were carried out for 24–36 min and at a light intensity of 1600 lx.

Two separate tests were carried out: (1) the frequency of encounters per minute in 24 consecutive 1-min intervals was compared to that expected from a Poisson distribution (Sokal and Rohlf 1969) to determine whether 'encounters' were distributed randomly over time (13°C and six prey/arena). Goodness of fit was checked with the Kolmogorov–Smirnov test (Siegel 1956); (2) encounter data were compared to predicted values derived from our mathematical model.

The Strike Field of a *Chaoborus* Larva

Apparent attack distances did not vary significantly between temperature treatments (ANOVA, $P = 0.36$), and the data were pooled. Prey size was regressed on attack distance but the coefficient of determination was not significant ($P = 0.62$). We grouped observations at 2-mm intervals along the larval body (the first and last intervals are open) and plotted all cases where apparent attack distance was >1 mm (Fig. 1). In this way, biases due to the effect of the contour of the body of the larva on apparent attack distances were eliminated. It was then possible to carry out statistical comparisons for data collected towards the outside of the attack field of the larva and determine the configuration of this field.

The mean values from the seven different regions did not vary significantly (ANOVA, $P = 0.64$) suggesting that *Chaoborus* attacks at comparable distances along the entire body. Attack frequencies showed a marked decrease at distances greater than 2.2 mm from the longitudinal axis of the body of the larva (Table 1); this may represent a threshold value set by physiological and morphological limitations of the capture mechanism (personal observations suggest that larvae can detect prey at much greater distances). As visual observations in the laboratory indicate that a larva will attack prey above or below its body as well as to the side (except for dead spaces directly behind, directly in front, and just above its head), this threshold value determines a roughly cylindrical effective strike field for the *Chaoborus* larva. This is represented by the hatched line in Fig. 1. It includes 93% of all attacks observed on high-speed films in the laboratory. The dotted line (drawn 2 mm away from the surface of the body of the predator) also includes 93% of all attacks recorded on film. The latter definition was most practical to collect visual observations of predator–prey interactions in the laboratory, and was used in testing the model.

Designing the Encounter Model

ASSUMPTIONS OF THE MODEL

We will consider the encounter process between a stationary cylinder and spheres which are randomly distributed and move at constant velocity in random directions. First we examine the plausibility of these assumptions:

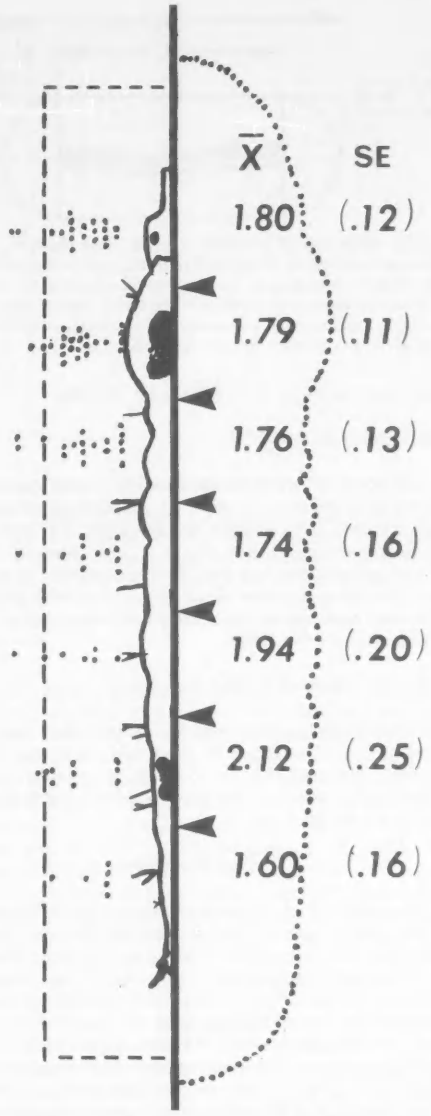

FIG. 1. Position of copepods (projected onto the horizontal plane through the predator when filmed from above) at the moment of attack by the 4th instar larva of *C. trivittatus*. The data (left and right sides pooled) are grouped at 2-mm intervals (between arrows) along the larval body. Apparent attack distance is measured perpendicularly from the long body axis to the nearest position of the prey at the time of attack. Only values >1 mm have been considered. The means are given for each interval (with standard errors). The hatched and dotted lines circumscribe areas which include about 93% of all observations.

The predator is stationary — Whether the movements of the larva will affect predicted rates of encounter will depend on the amount and rate of displacement. Observations in the laboratory suggest that 4th instar larvae of *Chaoborus* do not 'search' or 'stalk' extensively and that relatively low speeds (<1 mm/s; Pastorok 1978; Gerritsen 1980; Giguère personal observation) are involved. These are small relative to the speed of the prey (Swift and Fedorenko 1975), and Gerritsen (1980) has shown that the greater of two speeds (viz. predator and prey) has the stronger effect in determining encounter rates.

TABLE 1. Frequency of attack on copepods by the 4th instar larva of *C. trivittatus* as a function of apparent attack distance (see Fig. 1).

Apparent attack distance (mm)	No. of observations
0.00–0.20	29
0.21–0.40	12
0.41–0.60	17
0.61–0.80	19
0.81–1.00	15
1.01–1.20	27
1.21–1.40	17
1.41–1.60	9
1.61–1.80	11
1.81–2.00	4
2.01–2.20	13
2.21–2.40	4
2.41–2.60	1
2.61–2.80	1
2.81–3.00	3
3.01–3.20	2
3.21–3.40	0
3.41–3.60	0
3.61–3.80	0
3.81–4.00	2

Prey are spherical — While this approximation appears reasonable for copepods swimming in straight path segments (see below), prey of different shapes may not be so easily incorporated into the model. It is difficult to determine the equivalent spherical size of prey over a wide range of prey size or length. One factor mitigates this problem. Prey swimming speeds are often strongly positively correlated with prey size (Eq. 5 below; Swift and Fedorenko 1975), and the model should be most responsive to changes in swimming speed of prey as prey size increases, as long as the prey are considerably smaller than the predator. Small errors in estimating the effective size of prey will then be negligible by comparison.

Prey swim at constant speed and in random directions — Movement patterns of copepods include rolls, loops, sudden jumps, sprints for fast escape, chases related to sexual behavior, etc. Based on observations in the laboratory, their predominant locomotory behavior consists of relatively slow displacements along straight path segments (while 'filter-feeding') interspersed with sudden jumps or changes of direction of short duration. This would result in a log-normal speed distribution, and cause at most a 3–4% error in calculating encounter rates (Gerritsen and Strickler 1977). As this pattern of behavior generally involves movement at constant speed and frequent changes in swimming direction, it should result in prey approaching the strike field of the predator from random (or unpredictable) directions.

Prey are randomly distributed within a patch — This condition might hold for a small patch (see Discussion). To test the model, however, the tendency of predator and prey to aggregate near water–Plexiglas interfaces must be accounted for. Giguère (1981) showed that the extent to which predator and prey aggregate near Plexiglas walls in the arenas is nearly compensated for by the fact that a wall prevents prey from approaching a predator from a particular direction. He derived a simple correction factor (1.035) for these arenas, and we therefore multiplied the encounter data by this factor.

The Mathematical Derivation

We will derive a general formulation of the encounter problem for a stationary cylinder of length L and radius R, and spheres of radius r which are uniformly distributed and move at constant velocity in random directions. From Gerritsen and Strickler's (1977) eq. 7, we find that the rate of encounter (E) between prey (considered as dimensionless points in space) and a motionless predator with a spherical encounter field (radius R) is:

$$(1) \quad E = n\bar{s}\,\pi R^2$$

where $\bar{s}$ represents the average speed of the prey and n the density of the prey. The term πR^2 is the cross-sectional area of the encounter field of the predator. However, the cylindrical encounter field of *Chaoborus* will present a different cross-sectional area depending upon the prey's position relative to the predator. Thus we replace πR^2 by the average cross-sectional area ($\bar{A}$) of a cylinder of length L and radius R', to which hemispherical ends were added (Fig. 2). Notice that spherical prey with radius (r) are now considered dimensionless, their size being included in that of the strike field of the predator, i.e. $R' = R + r$. The average cross-sectional area is then the area of a circle, $\pi R'^2$, plus the average area of a rectangle, $\pi(R'L/2)$. The appropriate encounter formula then becomes:

$$(2) \quad E = n\bar{s}\,\pi\left(\frac{R'L}{2} + R'^2\right).$$

This expression can be simplified further. Let L_t be the total length of the encounter field, such that $L = L_t - 2R'$, and substitute in Eq. 2. Then,

$$(3) \quad E = n\bar{s}\,\pi\left(\frac{R'L_t}{2}\right).$$

Model Parameters

To compare the output of the model to encounter data collected in the laboratory, we must choose appropriate parameter values for the model. The characteristic dimensions of the cylinder representing the strike field of the predator can be established as L_t = 18 mm and R = 2.2 mm (see Fig. 1 and Table 1).

The diameter of the spheres (d) was set equal to the maximum width (mw) of a copepod measured in the cephalic area under a binocular microscope. For *D. kenai* and *D. leptopus*,

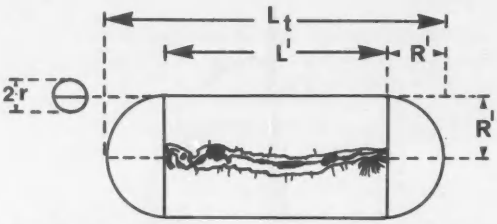

FIG. 2. Side view of a cylinder of length L and radius R'. These dimensions are that of the strike field of the predator augmented by the radius (r) of the prey. L_t represents the total length of the cylinder after hemispherical ends of radius R' are added. The solution of the encounter problem requires an estimate of the average cross-sectional area ($\bar{A}$) of this cylinder. See text for explanation.

this relates to length (l) as follows (r^2 = 0.98):

$$(4) \quad \text{mw} = 0.3456l^{0.8354}.$$

The speed of copepods (*D. kenai* only) was determined from high-speed films (see Materials and Methods) of individuals traveling along straight path segments. The data were grouped according to prey size at 0.2-mm intervals, and a polynomial equation was fitted by a least-squares method to the mean of each group. Since group sizes were unequal, this was preferred to fitting individual data points. The relationship is (r^2 = 0.94):

$$(5) \quad \bar{s} = -0.53 + 2.15l - 0.153l^2.$$

This formula is approximate as it ignores stops and quick bursts of speed exhibited by diaptomid copepods. Nevertheless it represents the overall conditions prevalent in this system and is consistent with the data of Swift and Fedorenko (1975) for the same species.

Testing the Model

The agreement of observed encounter frequencies during 1-min intervals with predicted values from a Poisson distribution was good (Kolmogorov–Smirnov, $P \geq 0.20$). However, large copepods (category IV) may have encountered the strike field of the larvae in a somewhat clumped manner. As this could be related to some form of sexual behavior enhanced by the high densities of adult copepods used in these experiments, more data were obtained at low densities (two replicates at 13°C with one, two, and three prey/arena). None of the data ($P \gg 0.20$) indicate that copepods encounter the strike field of a *Chaoborus* larva in a nonrandom fashion over time. Note that although this finding increases the plausibility of our model, it is not a test of the assumption that prey swim in random directions (i.e. this pattern could occur even if prey swim predominantly in one plane).

There were no significant differences between the rate at which prey encountered the strike field of a *Chaoborus* larva at 13 vs. 24°C (two-tailed paired t-test; $P \geq 0.90$). The data therefore were pooled and analyzed in a two-way ANOVA (Sokal and Rohlf 1969). There was no interaction between

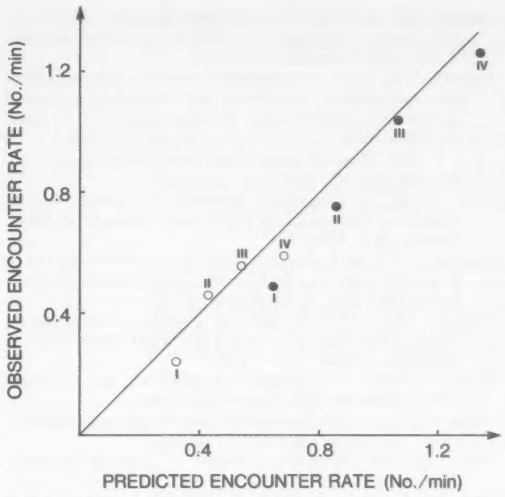

FIG. 3. Graphic representation of observed vs. expected encounter rate values of *Chaoborus*–copepod interactions based on visual data collected in the laboratory and predictions generated from the model, respectively. The line would represent a perfect fit. We show results for copepod size categories I to IV (see Materials and Methods) at two prey densities (open circles: three prey/arena; closed circles: six prey/arena).

prey size and prey density ($P = 0.28$), but there were significant positive effects of prey size ($P \leq 0.0001$) and prey density ($P = 0.001$) on E. The data were multiplied by 1.035 (see assumption 4 above) and compared to the predictions derived from our model for the same density and prey size categories (Fig. 3). The fit is striking when one considers that the theoretical model was derived independently. The error varied from −6.3 to 17.2% for categories II, III, and IV, but values as high as 20.1 and 37.0% were obtained for category I. As the latter category was comprised of *D. leptopus*, and Eq. 5 (for copepod speed) applies to *D. kenai* only, the estimates for swimming speed may have been erroneous. We therefore conclude that our model is consistent with laboratory data given proper input parameter values.

Discussion

We have shown that the *Chaoborus* larva possesses an approximately cylindrical strike field, and have derived a collision model which takes this into consideration. The model predictions agree well with observations collected in the laboratory (i.e. the rate at which copepods approach within 2 mm of the body of the larva). Furthermore, the data indicated a random pattern of distribution of 'encounters' over time when copepods were used as prey. These experimental verifications lend support to the model.

However, the usefulness of the model is limited by our definition of 'encounter,' which does not take into account prey detection by the predator. As we know that (a) prey will pass through the strike field of a larva without being attacked (Giguère 1981) or possibly even detected, and (b) probabilities of attack are not uniformly distributed within the strike field of the *Chaoborus* larva (more attacks occur near the anterior portion of the body of the larva, Fig. 1), we cannot predict feeding opportunities from a predator's standpoint.

It is possible to determine empirically (through visual observations) what proportion of 'encountered' prey are actually attacked. Giguère (1981), for example, found that about 46% of copepods entering the strike field of the 4th instar larva of *C. trivittatus* are attacked, regardless of prey length (0.9–2.6 mm), prey density (one, three, four, or six prey/arena), or temperature (6, 13, or 24°C). As the proportion of attacks which result in prey capture has also been determined (Swift and Fedorenko 1975; Pastorok 1978; Giguère 1981), laboratory estimates of predation rates can be obtained for this larva.

To determine whether our model can predict *Chaoborus* feeding rates in a natural environment, other factors must be considered.

Prey Movements

For an ambush predator, it is possible to assess the importance of preferential swimming directions by prey (i.e. vertical and horizontal motion) to the encounter process by looking at the symmetry of the strike field of the predator. Giguère (1981) compared the encounter rates for prey which move in a vertical plane (from above and below) to that of prey moving in a horizontal plane, where prey can approach the predator not only from two sides but from the ends as well. He estimated that the encounter rate was ~20% greater in the latter case than in the former case. Our model would therefore underestimate encounter rate by 10% if prey are migrating vertically in one direction. If copepods move in both planes in various proportions, a smaller difference will result.

Heterogeneous Prey Distribution

A major problem consists of defining an appropriate time scale and patch size while taking into account the tendency of prey to aggregate in specific areas (particularly on a vertical scale). A patch must be sufficiently small to yield a prey distribution that is fairly random, but not so small that a significant number of prey move in and out of it over short periods of time. In other words, one must define an instantaneous rate of encounter for a predator entering a new patch, and apply the model successively as the predator travels from patch to patch over time. The relevant scale of predation dynamics should be determined by potential directional movements of the predator or the prey, e.g. vertical travel.

Fortunately, two factors reduce the problems of applying the model to real situations: (1) predator and prey live in a relatively uniform environment; and (2) larvae attack in response to acoustic stimuli produced by their prey, and the propagation of these signals in water is not altered greatly by biotic or abiotic factors in the environment (in contrast to the situation for visual predators, Giguère 1980, 1981). Thus the model may be used to solve encounter problems for larvae in a natural environment, although this will require extensive knowledge of predator and prey distributions in the field.

The present formula estimates the encounter rate between moving spheres and a stationary cylinder. This approach can be applied to volumes of different shapes (e.g. cone, ellipsoid, etc.). Thus, one can solve encounter problems for other organisms living in a fluid environment. Many predators lie in ambush until the prey comes within a short distance and then launch an attack to subdue it (e.g. chaetognaths, Feigenbaum 1979). The size and shape of their strike field will depend on the anatomy and physiology of the capture mechanism, and non-spherical encounter models will often be necessary.

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An Empirical Model to Estimate the Relative Importance of Roots in Phosphorus Uptake by Aquatic Macrophytes

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A simple empirical model for predicting the relative contribution of roots in phosphorus uptake by submersed macrophytes is presented. The model requires only approximate dissolved reactive phosphorus (DRP) concentrations in the sediment pore water and overlying water as inputs and can explain 97% of the observed variance. It has the form: $P = 99.8/1 + 2.66\ (s/w)^{-0.83}$ where P is the relative contribution of the root in phosphorus uptake, s and w are the pore water and overlying water DRP concentrations, respectively. The nonspecificity of the model makes it readily applicable to environmental problems related to the role of macrophytes in phosphorus cycling and suggests a similar phosphorus uptake behavior for morphologically different species.

Key words: macrophytes, phosphorus, empirical model

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L'auteur décrit un modèle empirique simple permettant de prédire la contribution relative des racines dans l'assimilation du phosphore par des macrophytes submergés. Comme entrées, le modèle ne requiert que les concentrations approximatives de phosphore réactif dissous (DRP) dans l'eau des pores du sédiment et dans l'eau sus-jacente, et il peut expliquer 97 % de la variance observée. Le modèle a la forme suivante : $P = 99{,}8/1 + 2{,}66\ (s/w)^{-0.83}$ où P est la contribution relative de la racine dans l'assimilation du phosphore, s et w sont les concentrations de DRP dans l'eau interstitielle et l'eau sus-jacente, respectivement. Parce qu'il n'est pas spécifique, le modèle peut facilement s'appliquer aux problèmes environnementaux liés au rôle des macrophytes dans le cycle du phosphore. D'après ce modèle, il y aurait chez des espèces morphologiquement différentes un comportement semblable d'assimilation du phosphore.

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SEVERAL investigators have estimated the relative contribution of roots and shoots in phosphorus uptake by submersed macrophytes under various experimental conditions (Littlefield and Forsberg 1965; Bristow and Whitcombe 1971; Denny 1972; Schults and Malueg 1971; DeMarte and Hartman 1974; Seadler and Alldridge 1977; Gabrielson 1978; Welsh and Denny 1979; see also Table 1). So far, many species, representing a wide range of morphological features such as root-to-shoot ratio, leaf dissection, and general growth form have been studied. Although most authors measured phosphorus uptake from tracer (^{32}P and/or ^{33}P) assimilation rates, the techniques used were extremely variable. Incubation periods ranged from hours to months; the plants were either sectioned or left intact; rooting substrates were either water, sand, or mud and phosphorus concentrations supplied to shoots or roots varied by orders of magnitude. Moreover, the results obtained from these studies were expressed in many different ways such as rates of phosphorus uptake per plant, per unit weight of plant, or as counts per minute and concentration factors, thus making difficult their comparative analysis.

Carignan and Kalff (1980) measured the relative contribution of roots and shoots in phosphorus uptake in situ by three species of submersed macrophytes grown in three sites characterized by different sediment and water phosphorus availabilities. On the basis of the similarity of results obtained for the three species, they suggested that a simple nonspecific predictive model linking the relative importance of roots and shoots in phosphorus uptake to the relative availability of phosphorus in sediments and overlying waters could be constructed. The existence of such a model would significantly contribute to our knowledge of the role of macrophytes in phosphorus cycling.

Many factors could hypothetically affect root vs. shoot uptake. Among those frequently suggested are shoot/root

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biomass or area ratio, relative availabilities of phosphorus in water and sediments, species involved, temperature, and light. However, a model is more useful if it contains few, easily accessible inputs, and is still reasonably accurate. In this paper, a simple model is presented which relates phosphorus uptake by root vs. shoot to the relative dissolved reactive phosphorus (DRP) concentrations in the sediment pore water and overlying water.

Methods

Selection of Data

Because only quantitative estimates of the root or shoot contribution in phosphorus uptake could be used to construct the model, valuable studies showing the dependence of macrophyte on sediments (Denny 1972; Best and Mantai 1978) could not be used. Only those studies where phosphorus uptake was measured as tracer uptake were retained and the following set of criteria were applied for the selection of data:

i) The measurements had to be done on plants recently collected from natural sites, thus exhibiting a natural shoot-to-root ratio, or on plants grown long enough under artificial conditions to allow for the development of normal shoot and roots. According to this criterion, the results of Bristow and Whitcombe (1971) could not be used.

ii) The DRP concentration of the medium in contact with the shoots and roots (whether natural or artificial) had to be specified. Consequently, the results of DeMarte and Hartman (1974) and some results of Bole and Allan (1978) could not be used.

iii) The results, when expressed as rates of ^{31}P or ^{32}P uptake per unit weight of plant material, had to be transformable in units of ^{31}P uptake per total plant (root + shoot). Thus, the results of Littlefield and Forsberg (1965), Seadler and Aldridge (1977), and Welsh and Denny (1979) could not be used. Although McRoy et al. (1972) did not specify the root and shoot biomasses of their experimental plants, they reported mean values for *Zostera* occurring at their study site which I used to transform their data into units of phosphorus uptake per plant.

iv) Macrophytes commonly sustain an active epiphytic community characterized by a high nutrient turnover rate (Allen 1971; Cattaneo and Kalff 1980; Carignan and Kalff 1981). Short-term ^{32}P-uptake measurements are therefore likely to be overestimated if no precautions are taken to remove epiphytes or to correct for shoot uptake due to epiphytes. Consequently, the data of Schults and Malueg (1971) were not included because they apparently did not consider epiphytic phosphorus uptake.

Root vs. Shoot Uptake Experiments

The relative importance of roots and shoots in phosphorus uptake by three species (*Myriophyllum spicatum*, *Heteranthera dubia*, and *Vallisneria americana*) was measured in situ under a low (1:1) pore water:overlying water DRP concentration ratio using the method described in Carignan and Kalff (1980). Briefly, sprouting plants (5−10 cm) were grown in situ to maturity (6−10 wk) in ^{32}P-labeled sediments of known available P specific activity, with the shoots in free contact with the unlabeled ambient water. After harvesting, the contribution of the root in phosphorus uptake was calculated as the ratio of plant phosphorus to available sediment phosphorus specific activities. Conditions of low pore water phosphorus:overlying water phosphorus were induced by growing the plants in a hypertrophic site (Rivière du Sud), but rooted in nutrient-poor sediments (Memphremagog Central). Both sites are described in Carignan and Kalff (1980).

Analysis of Data

Although the preceding limitations excluded almost half of the available data on phosphorus uptake by macrophytes, nine studies performed on 15 species remained and were used to construct the model. All the data were transformed into percentage of contribution by the root in total phosphorus uptake by the plant and plotted against pore water DRP:overlying water DRP concentration ratio. Each individual datum shown in Table 1 was given an equal weight even if some measurements were statistically more meaningful than others.

A log-sigmoid model of the form $y = C/(1 + Ax^{-B})$, where y is the percent uptake by the roots, and x is the sediment pore water/overlying water DRP ratio, was assumed. The value and variance of parameters A, B, and C were found by computer iteration using a Levenberg−Marquardt finite difference algorithm (IMSL). The variance of $\hat{y}$ and 95% confidence interval of the regression were approximated by a large sample variance maximum likelihood method (Kendall and Stuart 1973).

Pore Water DRP Profiles

The pore water of sediments colonized by macrophytes was sampled by dialysis with a compartmented sampler (Hesslein 1976) fitted with a biologically inert membrane (Gelman DM-450 or HT-450). The samplers were left in the sediments for 10−15 d to equilibrate, then retrieved, and the content of each compartment quickly injected in pre-acidified vials. DRP was measured within 48 h by an automated method (Stainton et al. 1974).

Results and Discussion

Uptake Experiments

Macrophytes grown in situ under a pore water/overlying water DRP concentration ratio approximately equal to unity derived from 28 to 36% of their phosphorus from the sediments (Table 1). This range is surprisingly limited considering the large morphological differences existing between *Myriophyllum*, *Vallisneria*, and *Heteranthera*. The proportion of sediment-derived phosphorus found in the root (31−48%) was significantly higher ($P < 0.05$, t-test) than the proportion found in the shoot alone (21−32%), or in the whole plant. These values are comparable to those reported in the literature for plants, including other species, experimentally subjected to root and shoot media having a 1:1 DRP ratio: *M. spicatum* (18.7%), *Vallisneria spiralis* (21.4%), and *Zostera marina* (26.1%).

TABLE 1. Relative importance of roots in phosphorus uptake by 12 species of aquatic macrophytes. Values are rates of ^{32}P or ^{33}P uptake under various experimental conditions. DRP: dissolved reactive phosphorus.

Source	Species	Method	DRP ($\mu g \cdot L^{-1}$) Root medium	DRP ($\mu g \cdot L^{-1}$) Shoot medium	% uptake by root mean ± SE
Penhale and Thayer (1980)	*Zostera marina*	12-h incubation in partitioned containers	200	3	98.9
McRoy and Barsdate (1970)	*Z. marina*	50-h incubation in partitioned containers	25	25	26.1
McRoy et al. (1972)	*Z. marina*	20-h incubation in partitioned containers	2000	30	93.2[a]
Gentner (1977)	*Vallisneria spiralis*	24-h incubation in partitioned containers	30	30	21.4
Bole and Allan (1978)	*Myriophyllum spicatum*	Grown 40 d on labeled sediments	300	2000	8.0
Smith (1978)	*M. spicatum*	Seasonal average of 15-min incubations of roots or shoots	150	5	73.0
Waisel and Shapira (1971)	*M. spicatum*	24-h incubation in partitioned containers	3100	3100	18.7
Twilley et al. (1977)	*Nuphar luteum*	24-h incubation in partitioned containers	124	50	73.0
Carignan and Kalff (1980)	*Myriophyllum spicatum*	Grown in situ 8–12 wk on labeled sediments	1490	167	Whole 70.0±0.5 Shoot 66.7±1.3 Root 85.4±2.1
"	*M. spicatum*	"	1200	1.9	93.2
"	*M. spicatum*	"	169	0.5	99.4±0.5
"	*Vallisneria americana*	"	1490	167	Whole 74.2±2.7 Shoot 69.4±2.8 Root 81.1±2.7
"	*V. americana*	"	1200	1.9	86.0±2.0
"	*V. americana*	"	169	0.5	103.1±5.6
"	*Heteranthera dubia*	"	1490	167	Whole 70.3±1.2 Shoot 68.7±1.3 Root 84.8±1.7
"	*Myriophyllum alterniflorum*	"	169	0.5	104.4±1.0
"	*Potamogeton zosteriformis*	"	"	"	107.4±2.3
"	*P. foliosus*	"	"	"	98.6±2.1
"	*Callitriche hermaphroditica*	"	"	"	94.2±2.4
"	*Elodea canadensis*	"	"	"	99.0±2.5
"	*Najas flexilis*	"	"	"	100.8
Carignan (this study)	*Myriophyllum spicatum*	"	174	167	Whole 33.0±3.2 Shoot 28.5±2.4 Root 48.7±4.2
"	*Vallisneria americana*	"	"	"	Whole 28.0±1.1 Shoot 21.0±1.1 Root 31.0±1.3
"	*Heteranthera dubia*	"	"	"	Whole 36.0±2.9 Shoot 32.0±2.3 Root 46.2±2.0

[a]Assuming a 65:35% biomass distribution for above ground:below ground structures.

MODEL OF PHOSPHORUS UPTAKE

The best fitting relation found between the relative importance of root and shoot in phosphorus uptake and relative phosphorus availability was as follows (Fig. 1):

$$P = \frac{99.8}{1 + 2.66(s/w)^{-0.83}} \qquad r^2 = 0.97,\ N = 25$$

where P is the percent contribution by the root to whole plant phosphorus uptake, s and w are the pore water and overlying water DRP concentrations, respectively. *Nuphar luteum* (Twilley et al. 1977) lay far above the regression line and was excluded from the data set. Because it is a floating leaved plant, upward nutrient translocation is probably facilitated by evapotranspiration. When the contribution of the sediment-derived phosphorus to the phosphorus content of the shoot alone is considered, data originating from short-term radiotracer-uptake experiments cannot be included because upward translocation of nutrients assimilated by the root is not instantaneous. The relation then becomes (Fig. 2).

$$P = \frac{99.9}{1 + 2.79(s/w)^{-0.83}} \qquad r^2 = 0.94,\ N = 19.$$

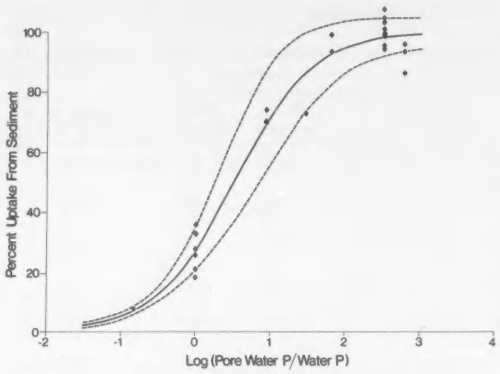

FIG. 1. Total plant (shoot + root) relative phosphorus uptake from sediment or root medium versus pore water/overlying water DRP ratio (log scale). The broken lines represent the 95% confidence interval for predicted values.

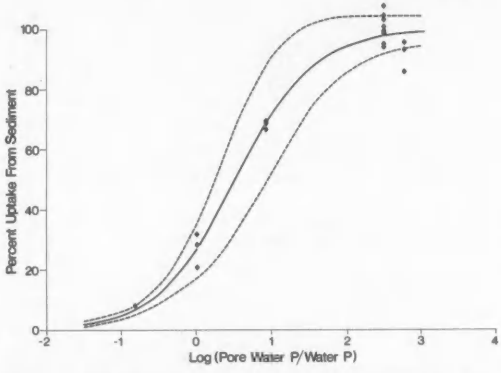

FIG. 2. Relative phosphorus uptake from sediment when shoot alone is considered. Broken lines as in Fig. 1.

One of the basic problems associated with the evaluation of the role of aquatic macrophytes in phosphorus cycling is the relative importance of root vs. shoot in phosphorus uptake. This will, to a large extent, determine whether macrophytes should be considered as sources or sinks of phosphorus in a particular system. The simplicity of the proposed model should facilitate this estimation because it requires only sediment pore water and overlying water DRP concentrations as inputs. Pore water DRP concentration found in sediments colonized by macrophytes can show important vertical (Fig. 3) and seasonal variations often induced by root uptake (Carignan unpublished data). Such marked variations might appear to make the use of the model questionable without good information on rooting depth. However, it can be seen that the model is relatively insensitive to variation or errors in pore water DRP measurements. For example, given an open water and pore water DRP concentration of 10 and 50 $\mu g \cdot L^{-1}$, respectively, the model predicts 59% uptake by the root

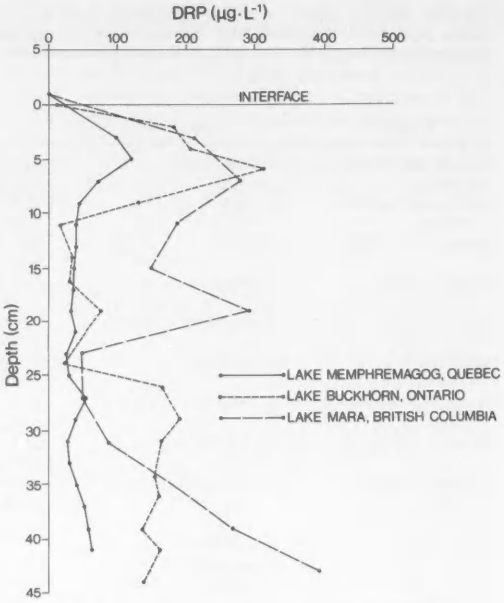

FIG. 3. Typical midsummer DRP profiles in macrophytes colonized sediments. *M. spicatum* was dominant in the three sites.

whereas a pore water DRP concentration of 250 $\mu g \cdot L^{-1}$ generates 84%. Thus, a fivefold change in pore water DRP concentration resulted only in a 25% difference in relative uptake by the root.

In spite of the large methodological and taxonomical differences between studies, there is a very good agreement between the observed values of relative contribution by the root and those predicted by the proposed model. Denny (1972) suggested that morphological characters such as root/shoot biomass ratio and vascular differentiation might play an important role in determining the major site of nutrient absorption in aquatic macrophytes. The observations presented here do not support this hypothesis because under similar phosphorus availability conditions, different species appear to behave similarly.

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Behavior of Atlantic salmon (*Salmo salar*) During Suspended Migration in an Estuary, Sheet Harbour, Nova Scotia, Observed Visually and By Ultrasonic Tracking

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BRAWN, V. M. 1982. Behavior of Atlantic salmon (*Salmo salar*) during suspended migration in an estuary, Sheet Harbour, Nova Scotia, observed visually and by ultrasonic tracking. Can. J. Fish. Aquat. Sci. 39: 248–256.

The movements of adult Atlantic salmon (*Salmo salar*) were followed in an estuary from August to November 1978 and in July and August 1979 by ultrasonic tracking. During these periods, the proportion of time spent by salmon in apparent random movement inside a small area steadily increased, reaching 97 or 98% in September and October, and then declined. This behavior was observed visually in schools of 17 to 75 salmon which showed no preference for sun or shade, were not easily disturbed, kept a constant distance from the surface associated with the halocline, and were in currents too low to measure. As the frequency of this behavior increased, average ground speed of moving fish decreased. Suspended migrations of up to 3½ mo were recorded. Salmon planted as smolts in East River and returning as adults remained almost exclusively in the East River arm of the Y-shaped estuary. Salmon favored areas having water deeper than 3 m, but showed no preference for areas deeper than 5 m inside the 3-m contour. Moving fish showed a tendency to move upstream on a rising tide and downstream on a falling tide, but these movements could be reversed by high turbine flows at the mouth of East River. A means of removing ultrasonic tags from live salmon without injury was developed.

Key words: Atlantic salmon, estuary, migration, behavior, ultrasonic tracking

BRAWN, V. M. 1982. Behavior of Atlantic salmon (*Salmo salar*) during suspended migration in an estuary, Sheet Harbour, Nova Scotia, observed visually and by ultrasonic tracking. Can. J. Fish. Aquat. Sci. 39: 248–256.

Le dépistage ultrasonique a servi à suivre les mouvements de saumons atlantiques (*Salmo salar*) adultes entre août et novembre 1978 et en juillet et août 1979. Durant ces périodes, le pourcentage du temps que les saumons ont passé en des mouvements apparemment au hasard à l'intérieur d'une petite superficie a augmenté régulièrement, atteignant 97 ou 98 % en septembre et octobre, pour ensuite diminuer. Nous avons observé ce comportement à vue dans des bancs de 17 à 75 saumons qui ne montraient aucune préférence pour le soleil ou l'ombre, n'étaient pas facilement dérangés, maintenaient une distance constante de la surface associée avec l'halocline et se trouvaient dans des courants trop faibles pour être mesurés. À mesure qu'augmentait la fréquence de ce comportement, la vitesse-sol des poissons en mouvement diminuait. Nous avons observé des arrêts momentanés de la migration, allant jusqu'à 3½ mois. Des saumons ensemencés comme smolts dans la rivière East et retournant en eau douce comme adultes demeurèrent presque exclusivement dans le bras de la rivière East et dans l'estuaire en forme de Y. Les saumons montraient une préférence pour des régions où l'eau dépassait 3 m de profondeur, mais à l'intérieur du contour de 3 m ne montraient pas de préférence pour les régions de profondeur plus grande que 5 m. Les poissons en mouvement tendaient à se déplacer vers l'amont avec la marée montante et vers l'aval avec la marée baissante, mais de forts débits de turbines à l'embouchure de la rivière East pouvaient renverser ces mouvements. Nous avons mis au point une méthode d'enlèvement des marques ultrasoniques chez des saumons vivants sans les blesser.

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PASSAGE of Atlantic salmon (*Salmo salar*) through an estuary on their way to freshwater to spawn may be fairly prompt or quite slow (Elson 1975). Salmon in the Miramichi Estuary, whose movements were followed by Stasko (1975), included examples of fish moving many kilometres towards freshwater in a day and other fish which moved 2 km or less in 2 wk. Both patterns were observed in the same month, suggesting that the difference was not seasonally imposed. If some salmon normally spend some weeks or months in an estuary where they may be subject to predation and the effects of

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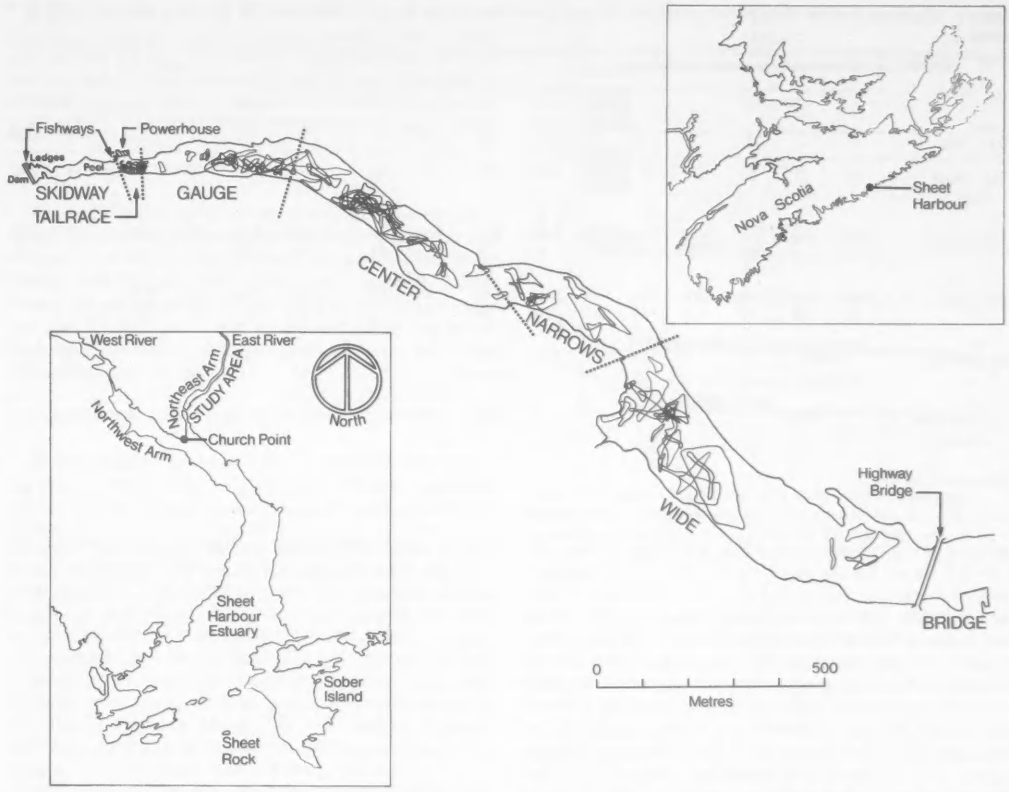

FIG. 1. The study area in the Northwest Arm of the Sheet Harbour Estuary with insets to show its location on the east coast of Canada and position with respect to the whole estuary. Subdivisions of the study area and, with the exception of the skidway area, all holding areas occupied by ultrasonic-tagged fish in 1978 and 1979 are shown.

pollution, it seems desirable to follow in detail the movements and so discover the localities occupied by these fish. The results of such an investigation using ultrasonic tracking methods and supplemented by visual observations of natural schools of fish in the Sheet Harbour Estuary are given here. To prevent disturbance of tagged fish a tracking method was devised which eliminated boat movements in their vicinity, and a method of tag recovery from live salmon was found which allowed reuse of tags without salmon mortality.

Factors which governed salmon movement from the Sheet Harbour Estuary to freshwater via the East River fishways from 1974 to 1979 were previously described (Brawn 1979).

Material and Methods

The Sheet Harbour Estuary is Y-shaped, its two arms each receiving the inflow of a salmon river (Fig. 1). Because of a hatchery stocking program involving the release of finclipped smolts in East River, it was possible to recognize fish released in East River and returning to the estuary as one- or two-sea-winter salmon. Ultrasonic tags were placed in the stomachs of some of these fish. An ultrasonic tracking technique was used which eliminated the need for boats to pass over the fish and permitted determinations of fish position every 5 min. The only access to East River from the estuary for salmon is by two fishways near the head of the tide. All salmon ascending the fishways enter traps at the top, and their age (in sea-winters) and origin (wild or hatchery) are recorded.

TELEMETRY PROCEDURES

Details of 19 salmon ultrasonic-tagged and 2 disc-tagged salmon are given in Table 1. All salmon, except one taken on a lure, were captured when teeth and fins became tangled in a 6-cm-mesh mackerel net across the skidway pool (Fig. 1). Salmon were held in a cage in the pool for a day or less before and after tagging to check their condition.

The salmon were tagged with ultrasonic tags designed by Dr D. G. Pincock (Nova Scotia Technical College, Halifax) with 50–73 KHz frequency, pulse repetition rates of 60–170 per minute, and a unique pulse rate–frequency combination for each tag. Tags were 6 cm long, 1.5 cm in diameter, and

TABLE 1. Minimum duration of suspended migration by East River salmon. (Fish 3, 13, 14 shed tags. Fish 11 and A were not heard after release.)

	1978 Sonic										1979					
											Sonic				Peterson	
Tags, fish	1	2	4	5	6	7	8	9	10	12	B	C	D	E	2002	2004
Fork length (cm)	51	57	55	62	52	53	49	54	54	55	74	52	57	54	54	51
Date caught	Aug. 2	Aug. 17	Aug. 23	Sept. 6	Sept. 6	Sept. 6	Sept. 6	Sept. 6	Sept. 6	Oct. 18	June 26	July 12	July 12	Aug. 1	July 12	July 25
Last heard	Sept. 29	Aug. 18	Aug. 31	Oct. 12	Oct. 13	Oct. 11	Oct. 20	Sept. 29	Oct. 4	Oct. 27	Aug. 31	Aug. 29	July 27	Aug. 27		
Up fishway	Date unknown				Oct. 26	Oct. 27	Oct. 23	Date unknown	Oct. 27		Oct. 12	Sept. 11			July 19	Sept. 17
Tag recovered at hatchery		Nov. 15						Nov. 15	Nov. 15							
Minimum time in estuary (d)	58	?	8	36	50	51	47	23	51	9	108	61	15	26	7	61

weighed 9.7 g in water in 1978 and were reduced to 4.8–5.5 cm by 1.4 cm and 9.1 g in 1979. In addition four Smith Root tags, frequency 75 KHz, 72–132 pulse rate, were used in 1978. All tags were smaller in proportion to fish length than the dummy transmitters shown by McCleave and Stred (1975) not to impede the swimming performance of salmon smolts. The activated ultrasonic tags were fitted with a smooth cap of epoxy resin and were inserted cap first into the stomach of salmon quieted in a solution of MS222 in estuarine water. While under MS222, all fish were measured and, in 1979, tagged with Carlin tags. The salmon were released after both fish and tag signal were found to be in satisfactory condition.

Fish position was determined by plotting the direction from which the ultrasonic signal was received by two hydrophones at separate points remote from the fish. The boat-mounted, hand-operated hydrophones were designed by Dr D. G. Pincock to be highly directional, having a resolution angle of 0.5–1.0°, and each bore a sighting device. To allow accurate boat positioning, the study area from bridge to barrier dam (Fig. 1) was marked at ~50-m intervals on each bank with 102 color-coded markers and then surveyed. Two observers in separate boats worked as a team, their boats anchored below separate markers on the bank across from the ultrasonic-tagged fish and so spaced that their lines of sight, when each hydrophone picked up maximum signal, would intersect at an angle not too acute for accurate fish positioning when the lines were plotted. The observers coordinated their observations by VHF receivers and every 5 min they simultaneously determined and recorded the point where the line of sight for maximum signal return intersected the bank between markers. The shore intersect positions were given in tenths of the distance between markers as judged visually. This information, plotted on maps to a scale of 1:2800 for the study area or 1:575 for fish within 300 m of the powerhouse, gave the position of the fish. Under the worst conditions of remoteness from the fish and obliqueness of intercept, an error of ±10 m could occur in determining the distance of the fish from the observers and of 2 m to either side of the line of sight, assuming a range resolution angle of 1°. A further error, not exceeding 2.5 m on either side of the line of sight, is introduced by recording the line of sight in tenths of between-marker distances. In 1978, from August 3 to November 17, every opportunity was taken to track individual fish and to spread the observations over as many fish as were present in the area from 08:00 to 17:00, Monday to Friday. Usually, the entire study area and, whenever weather permitted, the Northwest Arm and sea approaches were examined once or twice daily for the presence of ultrasonic-tagged fish. In 1979 tracking was carried out from June 13 to August 31, and when an entire rising or falling tide fell within daylight hours, the observers tracked a single fish for ½ h centred in each high-, ¾-, ½-, ¼-, and low-tide period. Otherwise in 1979 tracking was as in 1978.

Portable hydrophones were used to check for the presence of ultrasonic-tagged fish in the area of ledges below the dam and in the entrance to West River. Altogether fish were tracked at 5-min intervals for 113 h, 5 min in 1978 and 61 h, 45 min in 1979.

The greatest distance that a signal could be picked up was 1.2 km under ideal conditions in the Sheet Harbour Estuary. This signal range is large compared to the dimensions of the water bodies searched, which themselves then determine range, lending credence to the assumption that tagged fish which were not detected had left the area being searched. This assumption was made only if the signal was picked up again at a later date, proving transmission had not ceased.

Salmon ascending the East River fishways were inspected for ultrasonic tags, and tag removal from the live fish under MS222 was attempted with 31-cm round-ended specimen forceps. The tag was forced forward by pressure on the abdomen until just visible in the throat. In six fish extraction was attempted blindly as hand and forceps obscured the throat. However, tests on a freshly killed 53-cm salmon had shown

that tags could be removed if the forceps were forced 2 cm apart by a wedge 18 cm from their tips when the forceps made contact with the tag. This forceps–wedge method was used on three fish, and subsequent fish conditions were monitored at the Antigonish hatchery. Two of Dr Pincock's tags recovered in 1978 were fitted with new batteries for use in 1979.

Visual Observations

After mid-August 1978, the water was exceptionally clear. When the wind was light, salmon at a distance of 10 m could be seen and counted in the skidway area from the roof of the fishway buildings. All detailed visual observations were made from a raft anchored within 1 or 2 m of salmon groups in this area and totalled 7 h, 10 min spread over 9 d in August and September. Occasional observations of salmon in the tailrace were made from the bank.

Determination of Water Depth Preferences

Fish depth and total water depth were estimated visually in the skidway area and occasionally in the tailrace. Elsewhere, because the ultrasonic tags did not contain pressure-sensitive transducers, an indirect approach to depth preference was adopted. The tracking records disclosed the presence and extent of holding areas outside the skidway area, whose position could be related to water depth. Each holding area was examined to determine the proportion which lay over the depth zones 0–3 m, 3–5 m, and greater than 5 m, relative to chart datum. For the Northeast Arm, the area of each depth zone from the bridge, up to and including the tailrace, was determined. The observed distribution of fish relative to the depth of water available to them could then be compared to the distribution expected, based on the hypothesis that they showed no preference.

Physical Measurements

Twice daily readings of rainfall and air temperature at the powerhouse and complete records of turbine operation were made available by the Nova Scotia Power Corporation. In 1978, a tide gauge was installed 300 m downstream from the powerhouse and the records were analyzed to give the duration and height of the tides. Water depths were charted from the bridge to the lower third of the skidway section.

Results

Areas Occupied

In August 1978, ultrasonic-tagged fish occupied the sections of the study area and the Northeast Arm below the bridge fairly uniformly, with the exception of the skidway area which gave only 3% of the monthly records of occurrence (Fig. 2). On August 25, the only penetration of tagged fish into the Northwest Arm for 1978 was recorded. That day, two fish tags were detected, one tag no longer inside the fish had been shed 800 m into the Northwest Arm, and the other borne by a salmon 700 m into the Arm which, 6 d later, was detected for the last time at Sheet Rock, 8 km out to sea from Church Point (Fig. 1). On four occasions fish No. 1 could not

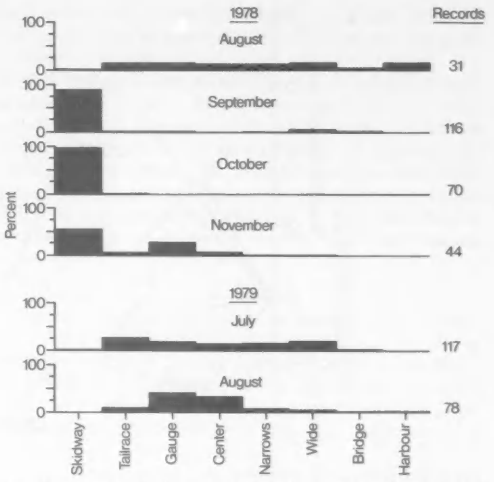

FIG. 2. Presence of salmon in each section of the study area in each month as a percentage of total records for the month. The presence of an ultrasonic-tagged fish in an area in the morning, afternoon, or evening is counted as a record. Harbour includes Northwest Arm and Outer Harbour.

be found in the study area, Northwest Arm, or outer harbor after extensive searches and was presumed to have gone to sea. It returned to the estuary on each occasion after an absence of 2 to 10 d, sometimes ascending the Northeast Arm to the powerhouse tailrace before disappearing again.

September and October 1978 were characterized by the concentration of salmon, including the ultrasonic-tagged fish, in the skidway area. In September, fish No. 1 ceased wandering and with four others was almost always in the skidway area. Another fish tagged and released at the skidway in September was missing, presumably at sea, for 18 d before rejoining the other tagged fish in the skidway for October. All these fish ascended the fishways, four in October and the fifth at an unknown date (silent tag recovered from hatchery).

The November records, which show fish no longer confined to the skidway area, were based on the tagging of two salmon in the 2nd week of November. The fish were observed pressed down among the stones on the bottom even until the falling tide exposed their backs. This behavior and their dark color suggested that they were spent fish.

In 1979 on June 29, salmon B, ultrasonic-tagged 2 d before, made the furthest recorded penetration of the Northwest Arm, to within 500 m of the West River outflow. This fish was subsequently tracked at frequent intervals, but was never again found in the Northwest Arm and ascended the East River fishway in October. The only other recorded entry of the Northwest Arm in 1979 took place in August when one fish moved 500 m from Church Point. Again, this fish was subsequently found only in the East River system.

Throughout July 1979, ultrasonic-tagged salmon occupied the study area fairly uniformly with the exception of the skidway area which was seldom entered. Fish were most frequently found in the powerhouse tailrace. In August, the chief difference between 1979 and 1978 was the total absence

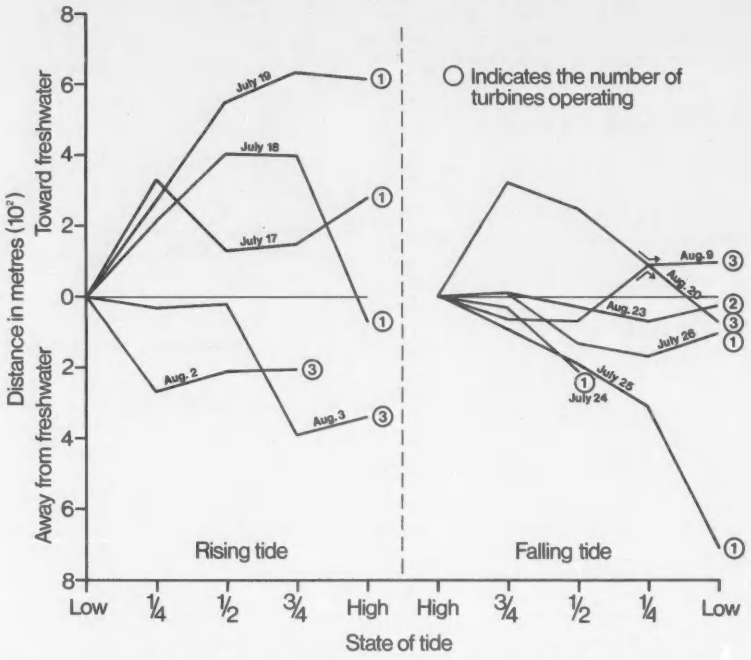

FIG. 3. Movements of salmon towards or away from freshwater relative to their position at low for rising and high for falling tides with varying numbers of powerhouse turbines operating.

of ultrasonic-tagged fish in the skidway area and the absence of the wandering behavior which in 1978 took fish below the bridge, into the harbor, and presumably to sea. Results with the mackerel net set in the skidway pool during June to August confirmed the almost total absence of salmon from this area.

In September and October 1979, no fish were seen in the skidway pool and, although not confirmed by ultrasonic tracking, it appears the absence of fish noted in August continued in these months. The July and August rainfall totalled 426 mm in 1979 against 82 mm in 1978, and unpublished observations since 1974 suggest that salmon congregate in the skidway pool only in dry summers.

None of the ultrasonic-tagged salmon ascended or attempted to ascend a fishway while they were being tracked.

MOVEMENTS AND TIDE

Analysis of all tracking records in relation to quarter-tide period failed to reveal any pronounced tendency for migration toward or away from freshwater associated with tidal period, rising or falling tide, or either slack water period. The 1979 data, based on ½-h samples of movements centered in each tide period likewise showed no clear direction of movement related to tide when considered as a whole. When plotted as displacements upstream or downstream relative to position at low tide for rising tides, and to high tide for falling tides, patterns apparently associated with number of turbines in operation emerged (Fig. 3). The displacements observed were small, averaging 254 m over entire rising or falling tides. A calculation of mean flow through the narrow section of the study area (Fig. 1) showed a net outflow at all states of tide with two or three turbines running, no outflow with rising tide and one turbine, and a net inflow only at rising tide and no turbines (Table 2). Water flow over the dam and down both fishways was insufficient to influence these net flows. In general, there was a tendency for fish to move toward the river with rising tide, but this was lost when three turbines, rather than one, were running (Fig. 3). The three turbines altered the mean velocity of flow at the narrows from zero to 0.03 m/s in an outward direction. A similar outward velocity resulted from the combination of falling tide and one turbine, and the tendency of slight seaward movement of the fish was the same. Further increase in outward velocity as more turbines were in operation on falling tide, rather than increasing the

TABLE 2. Mean velocities (m/s) of flow through cross section of the narrows under various tide and turbine flows. Inward flow +; outward flow −.

	No turbines	One turbine	Two turbines	Three turbines
Rising	+0.02	0.00	−0.02	−0.03
Falling	−0.02	−0.04	−0.06	−0.07
High/low tide	0.00	−0.02	−0.04	−0.05

seaward movement of fish, led to the salmon observed showing little displacement or moving landward. The apparent complexity of the response of salmon to tide and river discharge may explain the lack of correlation between tide and salmon movement found in the 1978 East River data.

Duration of Suspended Migration

The longest interval between tagging one salmon and its ascent of an East River fishway was shown by fish B, tagged on June 26, 1979, which came up the fishway $3\frac{1}{2}$ mo later (Table 1). Fish 2002 and 2004 were wild salmon taken, as were fish B and C, from the skidway pool, but externally tagged only. These four fish, taken from the same area over a 4-wk period in June and July, contained one early run fish and three which did not move to freshwater until September or October.

In 1978, fish were not available for ultrasonic tagging until August and September at which time, the 1979 results suggested, they may have been in the estuary for 1 or 2 mo. Many of these fish showed a period of 6 wk or more of suspended migration in spite of their late tagging.

Changes in Behavior with Time

All tracking data for 1978 and 1979 were analyzed for total time fish spent in a small area versus active movement from one place to another. There was a progressive decrease in the proportion of time spent in active movements from the beginning of July to the end of August 1979, and from the beginning of August to middle October 1978 (Table 3). After mid-October to November when the fall run finished in 1978, the proportion of time that fish spent moving again increased, but was still below the level seen in July to mid-August 1979.

Active Movement

When fish showed movement in a definite direction, minimum ground speed was calculated over 5-min intervals. The complexities of possible current patterns and fish paths precluded determination of actual swimming speeds, but changes in ground speed should reflect gross relative changes in swimming activity. In September and October, when salmon showed little inclination to move at all, average ground speeds were at their lowest (Table 3). Long individual tracks were infrequent, but two, such as fish B in July, showed average ground speeds of 63 and 62 cm/s over 1845 and 2040 m, respectively, the first at high tide moving upstream, the last at quarter-falling tide moving downstream.

Holding Behavior

Successive fish positions over an extended period sometimes occupied such a small circumscribed area that no significant measure of activity could be derived from them. There was also no tendency for successive points to show slow drift in one direction as would occur if randomly active fish were being displaced slowly by current. Such activity is described here as holding behavior.

The area occupied by fish showing this behavior was taken to be the area of the smallest possible circle which could be fitted over all points resulting from holding behavior of 25–45 min duration. The average area occupied (Table 3) showed a marked decrease from July to August and was less than 400 m^2 from September onwards. As holding behavior became more firmly established, the area occupied shrank. Compatible with this general picture of decrease in fish activity during the summer was the decrease in average ground speed of moving fish. Holding behavior occurred in all subsections of the study area (Fig. 1) and no physical factor appeared to confine the fish to the holding areas.

Direct observations of holding behavior were sometimes possible as in the tailrace in August 1978 when salmon in a group were observed for $2\frac{1}{2}$ h near the bottom, about 30 cm apart, and 2 m below the surface. These fish swam slowly to maintain position during this time and only rarely did any fish

TABLE 3. Monthly changes in the proportion of time spent by ultrasonic-tagged salmon in holding and moving behavior and in average area and ground speeds based on these two types of behavior, respectively.

	Tracking time (min)					Av. ground speed (cm/s)	Av. holding area (m^2)
	Holding		Moving		Total		
All tracking data 1979							
July 1st half	410	50%	411	50%	821	33	5200
July 2nd half	1214	79%	322	21%	1536	33	6500
Aug. 1st half	716	80%	178	20%	894	20	4000
Aug. 2nd half	436	96%	18	4%	454	40	2200
All tracking data 1978							
Aug. 1st half	396	71%	161	29%	557	38	2320
Aug. 2nd half	165	72%	65	28%	230	54	2750
Sept. 1st half	537	97%	15	3%	552	10	314
Sept. 2nd half	1381	97%	41	3%	1422	10	222
Oct. 1st half	1442	98%	35	2%	1477	5	335
Oct. 2nd half	950	97%	30	3%	480	9	327
Nov. 1st half	1345	86%	225	14%	1570	25	398

leave the group, leap, and return. By mid-August 1978, all salmon observed were in well-defined groups in the skidway area, although the fish bearing ultrasonic tags were not among them, resulting in a low value for skidway occupation for August (Fig. 2). No solitary salmon were seen. These fish were spaced fairly uniformly at any one time from 10 to 30 cm apart, in layers one to three fish deep, which moved up and down with the tide to maintain a fairly constant distance below the water surface varying from 0.3 to 2 m on different dates. The constant depth below the surface persisted even when the water was isothermal. Salinity at fish depth varied from 5 to 20‰ and temperature from 14 to 17°C. Fish avoided the freshwater layer. Water of higher and lower salinity not occupied by fish was present at the time of these observations.

There was no difference in depth occupied between fish in the shade and those in direct sunlight, nor was any response shown when cloud shadows passed. There was no tendency shown by groups partially in shade to move either into full sun or full shade, so local differences in light intensity apparently did not affect either the depth or the area occupied by salmon during the day.

In the absence of currents or movements of the group, the tendency to face in one direction was lost. Individual fish left the group to jump, or to rub one flank on rocks or the air/water interface and returned without disturbing the group. Both completely stationary group behavior and slow circling within a small area were observed. In every respect the group gave the impression of minimum energy expenditure and the area chosen rarely had currents sufficient to give a current meter reading. Stationary groups did not react to the sight of fluttering pages, or to sneezes, outboard motors, or an aluminum hull grinding on rocks within a few metres, but gave a brief startle reaction to the sight of a seagull overhead. When groups were moving slowly, slight avoidance responses were shown to stationary boats, but the original path was soon resumed.

After the 1st week in October 1978, fish observed were all moving swiftly and were easily frightened. After the fall run started on October 16, fish were found in groups of about 30 in freshwater in the skidway pool. They still occupied only small areas and these were not at the mouths of the two fishways or where any freshwater flowed into the estuary. In October 1978, the fall fishway ascents were largely made in response to artificial freshets which increased the flow passing the barrier dam and its fishway from 0.28 to 1.25 m^3/s (Brawn 1979).

Water Depth Preferences of Ultrasonic-tagged Fish

It was assumed that any preference for water greater than a certain depth would be expressed most clearly by salmon showing holding behavior as these fish are under no compulsion to occupy any particular area of the estuary whereas moving fish may cross many depth zones. There are two exceptions to this assumption at East River, and these ultrasonic tracking records were not considered in the analysis of water depth preference. Firstly, the ultrasonic-tagged fish in September and October 1978 occupied the skidway area exclusively, suggesting that some features of this area at this time were strongly attractive and the attraction might override any water depth preference. Secondly, data for both years showed that fish were attracted to the tailrace. On the basis of area alone, it was calculated that one holding area would be expected in the tailrace while 20 were recorded. These 20 holding areas were removed from further consideration by starting the analysis 40 m downstream of the powerhouse.

Salmon showing holding behavior in the rest of the study area showed a highly significant avoidance of water less than 3 m, chart datum, deep (Table 4). The proportion of the holding areas which occurred over water deeper than 3 m was distributed between 3-5 m and depth zones greater than 5 m almost in proportion to the respective areas of these zones (Table 4).

Although ultrasonic-tagged fish in general preferred water deeper than 3 m, there were examples of holding behavior in shallow water. In July, for example, a tagged fish remained for 25 min in water 1−1.3 m deep just upstream of the bridge.

Tag Removal

In September, practice tag recovery immediately following tagging using forceps blindly proved successful with a 54-cm salmon on the first and with a 59-cm salmon on the third attempt. Both fish were in good condition and released after 24 h. This method led to the death of fish 6, 8, B, and C in October. The forceps and wedge method enabled tags to be removed from fish 2, 9, and 10 in November at the Antigonish Hatchery. All fish survived in good condition until they were stripped of eggs or milt 3 wk later.

Removal of tags became progressively more difficult from September onwards as the stomach shrank. The tag cannot be seen while it is being grasped, and the force necessary to spread the forceps against the resistance of the throat

TABLE 4. Distribution of holding areas with respect to depth zone for the area from 40 m downstream of the powerhouse to the bridge. (*Represents 1 df.)

	Depth zone	Area, km^2	Tenths of holding areas			
			Observed	Expected	χ^{2}*	P
All holding areas	0−3 m	0.1241	306	434	78.1	<0.001
	3 m +	0.1166	534	406		
Holding areas inside 3-m contour	3−5 m	0.0783	363	358	0.21	>0.5
	5 m +	0.0383	171	176		

proved impossible to judge. Probing with the forceps improperly spread led to blood vessel damage and death, and only the use of a wedge gave the precision required for rapid tag withdrawal.

Discussion and Conclusions

All salmon visually observed in August and September and many in October formed distinct groups. Occasionally the tracking data showed that ultrasonic-tagged fish formed part of such a group, and it seems safe to assume that the movements shown by ultrasonic-tagged fish in an estuary in these months mark the movement of a group of salmon. Movements of the individual away from the group to rub on the bottom or jump were infrequent and brief. The distance of the jump from groups under observation was always within 4 and often within 2 m, so when salmon are showing holding behavior, the position of jumping fish indicates fairly accurately the group's location.

Salmon in groups showed schooling behavior in the sense that one fish reacted to others by remaining near them (Keenleyside 1955). Orientation in one direction, however, was externally imposed by water flow and was lost when the flow direction became uncertain.

Four salmon tagged during a 4-wk period in June and July 1979 which later proved to have contained one early and three late-run fish showed that late-run fish may be present in an estuary as early as June and in the same area as early run fish. Two of these fall-run fish were ultrasonic-tagged and with the exception of 1 d in the Northwest Arm, they remained in the study area at least until the end of August when ultrasonic tracking stopped. As both fish eventually ascended East River fishways it is presumed these fish remained in the estuary. It thus appears fall-run salmon may be present for $3\frac{1}{2}$ mo or more in an estuary. That fall-run salmon may be in an estuary at the time of the spring run and delay their further migration by three or more months has not been previously published, to my knowledge. It follows that tests to determine the toxicity of pollutants to salmon in estuaries should be based on exposure times of comparable duration. The presence of early and late-run salmon in an estuary at the same time may account for the movement towards freshwater of some salmon, but not others observed by Stasko (1975) in the Miramichi estuary.

Some salmon rivers have distinct early and late runs, and experimental selective breeding of these two groups from the Miramichi River, New Brunswick, showed that the time of return was genetically controlled (Elson 1973). That early and late-run East River salmon were both present in the estuary at the time of the early run suggests that the inherited differences in behavior and physiology which influence the timing of ascent operate while salmon are in the estuary. The behavior of salmon showing holding behavior was remarkable because of the completely passive condition of the fish which reduced energy expenditure to a minimum. The ability or lack thereof to assume this passive condition in the estuary may be the inherited difference between early and late-run salmon.

Salmon in the estuaries might be expected to favor areas of deep, cool water of high salinity during suspended migration but, although the East River area below the tailrace contained four long pools 6–8 m deep, holding fish were shown to be distributed inside the 3-m deep contour irrespective of water depth and did not favor these pools.

Salmon were present less frequently in water 0–3 m deep than in deeper water, but the depth data in shallow water did not allow zones less than 3 m deep to be distinguished, so the depth contour within which salmon presence occurs irrespective of water depth may be less than 3 m. Salmon observed visually maintained a constant distance from the surface unaffected by tide and by natural variations in light intensity. With an average high tide of 1.9 m above chart datum in the Northeast Arm, salmon must be within 5 m of the water surface or the observed presence in the 0- to 3-m zone could not occur. One salmon recorded in water of 1–1.3 m actual depth for 25 min must have been swimming within a metre of the surface.

Salmon groups directly observed in August and September avoided entirely fresh or highly saline water and occupied the halocline at salinities between 5 and 20‰. It is possible that salmon depth in an estuary is not an absolute value, but is determined by the depth of the halocline in the area.

In August 1978, an ultrasonic-tagged fish was absent from the estuary on four occasions and was almost certainly at sea, though perhaps only at the mouth of the estuary. On each occasion, the fish returned and ascended the Northeast Arm. Thus, it appears that salmon which have made a correct landfall, even if they return to sea, are able to return to their native river.

East River salmon showed a strong preference for the Northeast against the Northwest Arm of the estuary even during periods of suspended migration and in spite of the Northwest Arm having the larger area. The Northeast Arm accounted for 98% of the total records of fish present on a given date in these two areas. All records of ultrasonic-tagged fish entering the Northwest Arm were followed by records showing fish in the Northeast Arm or outer harbor so these fish did not migrate up West River. Thus, it appears that within an estuary common to several rivers, salmon remain in water influenced by the river they left as smolts, and suspended migration is not a period of investigating alternative rivers.

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Empirical Prediction of Fish Biomass and Yield[1]

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HANSON, J. M., AND W. C. LEGGETT. 1982. Empirical prediction of fish biomass and yield. Can. J. Fish. Aquat. Sci. 39: 257–263.

Data taken from the literature were used to develop and compare predictors of fish biomass and yield in lakes. Two new indices, total phosphorus concentration and macrobenthos biomass/mean depth, were the best univariate predictors of fish yield ($r^2 = 0.84$ and $r^2 = 0.48$, respectively) and biomass ($r^2 = 0.75$ and $r^2 = 0.83$, respectively) for four different data sets. Both new indices were stronger predictors of fish yield when compared to the morphoedaphic index, total dissolved solids, or mean depth for the same data set. The relatively constant relationship between fish biomass and macrobenthos biomass/mean depth implies a near-constant energy transfer from the benthos to the fish regardless of the number of fish species present.

Key words: biomass, yield, fish, macrobenthos, phosphorus, depth, dissolved solids, morphoedaphic index, lakes

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En nous servant de données extraites des travaux publiés, nous développons et comparons des prédicteurs de biomasse et de rendement de poisson dans les lacs. Pour quatre séries différentes de données, deux nouveaux indices, la concentration du phosphore total et la biomasse du macrobenthos/profondeur moyenne, sont les meilleurs prédicteurs unidimensionnels de rendement ($r^2 = 0{,}84$ et $r^2 = 0{,}48$, respectivement) et de biomasse ($r^2 = 0{,}75$ et $r^2 = 0{,}83$, respectivement) de poisson. Ces deux nouveaux indices sont de meilleurs prédicteurs de rendement en poisson que l'indice morpho-édaphique, les solides dissous totaux ou la profondeur moyenne pour la même série de données. La relation relativement constante entre la biomasse des poissons et celle du macrobenthos/profondeur moyenne laisse supposer qu'il y a transfert presque constant d'énergie entre le benthos et les poissons, quel que soit le nombre d'espèces de poissons présentes.

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PREDICTION of fish yield and biomass has long been a goal of fisheries managers, evidenced by the numerous attempts to formulate indices predicting these variables. Indices have been constructed in an attempt to predict fish yield from mean depths (Rawson 1952), total dissolved solids (Rawson 1951; Northcote and Larkin 1956), the morphoedaphic index (total dissolved solids/mean depth, Ryder et al. 1974), primary productivity and phytoplankton standing crop (Oglesby 1977b), and macrobenthos standing crop (Matuszek 1978). The utility and predictive power of these indices depend on constraints imposed by the range of mean depths, lake surface area, and total dissolved solids over which the indices apply, the effects of climatic and geographical regions, macrophyte beds, and difficulties in obtaining the necessary data (Ryder et al. 1974; and Oglesby 1977a, b). There have been few attempts to evaluate systematically the relative efficiency of these various indices for predicting fish yield based on a single data set. Matuszek's (1978) comparison of the relative power of mean depth, total dissolved solids, morphoedaphic index, and macrobenthos standing crop as predictors of fish yield represents an important first step. However, his analysis was weakened because he did not have complete data for net plankton and benthos standing crop in his data set.

Attempts to predict total fish biomass have been fewer in number, less comprehensive, and less successful. Moyle (1956) reported a positive relationship between fish biomass and total phosphorus in Minnesota lakes, and Jenkins (1967) discovered a significant correlation between morphoedaphic index and fish biomass in reservoirs, but the predictive power of the relationship was not strong ($r^2 = 0.40$). A marked improvement in predictive power was achieved when the reservoirs were subdivided by water use and chemical types before calculating the MEI/BIOMASS relationships ($r^2 = 0.27–0.54$; Jenkins 1967) and TDS/BIOMASS relationships ($r^2 = 0.63–0.81$; Jenkins 1977) again reflecting the need to constrain the data sets to achieve adequate predictive power.

The purpose of this study was twofold: (1) to compare

[1]A contribution of the Lake Memphremagog Project, Limnology Research Group, McGill University.

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systematically the relative power of the above-mentioned indices of fish yield and biomass; and (2) to develop and evaluate empirical predictors of fish biomass in lakes.

Data and Analysis

Fish Yield

Two data sets, having only four lakes in common, were constructed from the literature. Data set 1 consisted of 26 north-temperate lakes for which the surface area (km^2), mean depth (m), total dissolved solids (mg/L), macrobenthos standing crop (kg/ha, wet weight), and average fish yield (kg/ha, wet weight) were determined over the same time interval in each lake. Data set 2 consisted of 21 north-temperate lakes for which the surface area, total dissolved solids, mean epilimnetic total phosphorus concentration (μg/L), and average fish yield were determined over the same time interval in each lake. The time interval restriction was applied to ensure that lake conditions had not changed significantly between the time of determination of the various parameters in question. We were able to calculate the morphoedaphic index as an additional variable for all 43 lakes. A new variable, macrobenthos standing crop/mean depth, was tested because our reanalysis of Matuszek's (1978) data revealed a strong ($r^2 = 0.84$) and previously undetected linear correlation between 10- to 15-yr average fish yield (his "maximum sustainable yield") and macrobenthos biomass (his "BFWT") divided by mean depth.

The average fish yield data reported for the lakes in our data sets were derived from the long-term commercial and sport harvest for large lakes and from the sport catch for small lakes. Macrobenthos standing crop estimates consisted of the sums of weighted averages (by area) of the mean standing crops (wet weight) of all benthic invertebrates excluding microcrustaceans in the littoral, sublittoral, and profundal zones.

The range in reported values for the variables in the fish yield data sets was lake surface area 0.1−82 414.0 km^2; mean depth 2.4−148.0 m; total dissolved solids 24−279 mg/L; total phosphorus concentration 8−540 μg/L; macrobenthos standing crop 4.8−611.0 kg/ha; and average fish yield 0.40−42.0 kg/ha. The geographic distribution of the lakes was latitude 42°N to 62°N and longitude 17°E to 117°W.

Fish Biomass

Two additional data sets having no overlap with the fish yield data sets and only four lakes in common between them were developed from the literature. Data set 3 consisted of 20 lakes and ponds for which the surface area (ha), mean depth (m), macrobenthos standing crop (kg/ha, wet weight), and fish standing crop (kg/ha, wet weight) had been estimated. Data set 4 consisted of 14 lakes and ponds plus four pairs of averages for Minnesota lakes (Moyle 1956) for which the fish standing crop and mean epilimnetic total phosphorus concentration (μg/L) were reported. The relative efficiency of total dissolved solids and the morphoedaphic index as predictors of fish biomass could not be evaluated because the total dissolved solids were not reported for most lakes in data sets 3 and 4. Most fish biomass estimates were determined by whole lake or cover rotenone poisoning. The cover rotenone poisoning method for estimating fish biomass was validated by Hayne et al. (1967).

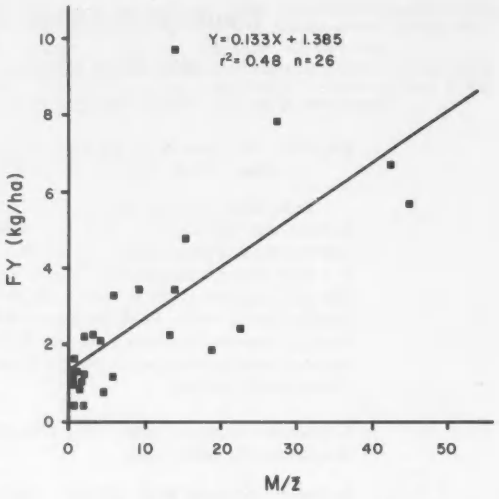

FIG. 1. Regression of fish yield (FY) on macrobenthos biomass (kg/ha)/mean depth (m) ($M/\bar{z}$).

The range of reported values for the variables in the fish standing crop data sets were lake surface area 0.1−25 000.0 ha; mean depth 1−33 m; total phosphorus concentration 10−557 μg/L; macrobenthos standing crop 6.5−181 kg/ha; and fish standing crop 2.6−859 kg/ha. The geographic distribution of the lakes in the data sets was latitude 0° to 56°N and longitude 121°E to 122°W.

A prime objective of this study was to compare the predictive power of the various indices. We therefore sought to maximize the proportion of the total variance explained (r^2) in the regressions we developed. In almost all instances this was achieved with linear regressions of untransformed data. Process-oriented researchers may correctly argue that the relationships we investigated are intuitively curvilinear and that log transformation will yield models that are more meaningful biologically. We have, therefore, included relevant regressions based on both transformed and untransformed data in the tables. The generally superior predictive power of the linear models we develop no doubt results from the fact that most data points used fall below the point where the system begins to saturate and the relationships plateau.

The complete data set used in these analyses and a bibliography of relevant references is available, at a nominal cost, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Canada K1A 0S2.

Results

Fish Yield

The best univariate predictors of fish yield in data set 1 (Table 1) were macrobenthos biomass/mean depth ($r^2 = 0.48$;

TABLE 1. Regression equations, based on data set 1, for estimating the fish yield (FY in kg/ha) from mean depth ($\bar{z}$ in m), lake surface area (Ao in km^2), total dissolved solids (TDS in mg/L), and macrobenthos standing crop (M in kg/ha). MEI = TDS/$\bar{z}$.

Simple regressions	r^2	P^a
(1) FY=0.133 M/$\bar{z}$+1.385	0.48	<0.001
(2) log FY=0.311 log M/$\bar{z}$+0.112	0.42	<0.001
(3) FY=0.012 M+1.293	0.47	<0.001
(4) log FY=0.487 log M−0.580	0.53	<0.001
(5) FY=0.013 TDS−0.096	0.36	<0.001
(6) log FY=0.757 log TDS−1.187	0.39	<0.001
(7) FY=0.002 MEI+2.664	0.00	<0.870
(8) log FY=0.298 log MEI+0.059	0.20	<0.025
(9) FY=−0.018 $\bar{z}$+3.224	0.07	<0.193
(10) log FY=−0.122 log $\bar{z}$+0.439	0.03	<0.444
(11) FY=−0.00001 Ao+2.801	0.01	<0.690
(12) log FY=−0.004 log Ao+0.230	0.0003	<0.930
(13) log M=1.335 log TDS−0.819	0.54	<0.001
Multiple regressions		
(14) FY=0.007 M+0.018 TDS−0.053 $\bar{z}$+0.00007 Ao+0.793 R^2=0.66 P^b<0.001		
(15) log FY=0.308 log M+0.372 log TDS−0.348 log $\bar{z}$+0.065 log Ao−0.736 R^2=0.61 P^b<0.001		
(16) FY=0.027 TDS−0.066 $\bar{z}$+0.00009 Ao+0.780 R^2=0.57 P^b<0.001		
(17) log FY=0.838 log TDS−0.446 log $\bar{z}$+0.059 log Ao−0.959 R^2=0.53 P^b<0.001		
(18) FY=0.011 M−0.066 $\bar{z}$+0.00006 Ao+1.990 R^2=0.55 P^b<0.001		
(19) log FY=0.463 log M+0.307 log $\bar{z}$+0.079 log Ao−0.375 R^2=0.58 P^b<0.001		

[a] t-test.
[b] F-test.

Fig. 1) and macrobenthos biomass (r^2 = 0.47). Total dissolved solids ranked third (r^2 = 0.36). Logarithmic transformation yielded no improvement in the explained variance in fish yield for these variables, but did improve the morphoedaphic index from a nonsignificant r^2 = 0.16 in the linear form to a significant r^2 = 0.20 in the logarithmic form. Mean depth and lake surface area were not significantly correlated with fish yield in linear or logarithmic form (Table 1). The best multivariate predictor of fish yield in data set 1 (R^2 = 0.66, Table 1) included macrobenthos biomass, total dissolved solids, mean depth, and lake area as independent variables. Removal of macrobenthos biomass or total dissolved solids (highly ranked univariate predictors of fish yield) from the multivariate regression resulted, respectively, in 9 and 11% reductions in the explained variance (Table 1).

The best univariate predictor of fish yield in data set 2 (Table 2) was total phosphorus (r^2 = 0.84; Fig. 2). Total dissolved solids ranked second (r^2 = 0.62) and was strongly cross-correlated with total phosphorus concentration (r^2 = 0.40). Mean depth, the morphoedaphic index, and lake surface area were not significantly correlated with fish yield (Table 2). Logarithmic transformation did not improve the predictive power of any of the variables. The best multivariate predictor of fish yield in data set 2 (R^2 = 0.97) included total phosphorus, mean depth, and total dissolved solids as the independent variables. Removal of total dissolved solids

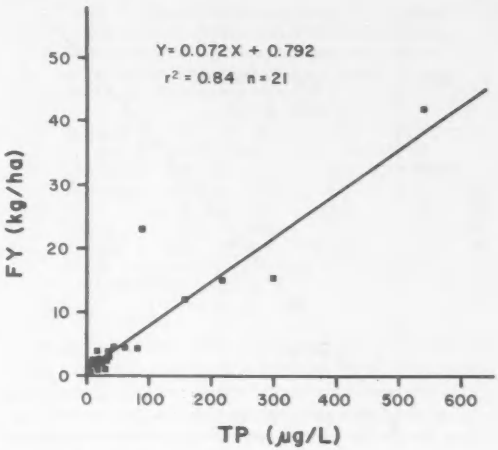

FIG. 2. Regression of fish yield (FY) on total phosphorus concentration (TP).

TABLE 2. Regression equations, based on data set 2, for estimating the fish yield (FY in kg/ha) from mean depth ($\bar{z}$ in m), lake surface area (Ao in km^2), total dissolved solids (TDS in mg/L), and total phosphorus concentration (TP in µg/L). MEI = TDS/$\bar{z}$.

Simple regressions	r^2	P^a
(1) FY=0.072 TP+0.792	0.84	<0.001
(2) log FY=1.021 log TP−1.148	0.87	<0.001
(3) FY=0.091 TDS−1.161	0.62	<0.001
(4) log FY=0.938 log TDS−1.214	0.39	<0.001
(5) FY=0.176 $\bar{z}$+4.412	0.14	<0.097
(6) log FY=0.665 $\bar{z}$−0.146	0.10	<0.059
(7) FY=0.225 MEI+3.820	0.10	<0.171
(8) log FY=0.311 log MEI+0.135	0.04	<0.371
(9) FY=−0.00006 Ao+6.670	0.00	<0.990
(10) log FY=0.004 log Ao+0.280	0.00	<0.930
(11) TP=0.936 TDS+0.890	0.40	<0.001
Multiple regressions		
(12) FY=0.066 TP+0.141 $\bar{z}$+0.013 TDS−1.513 R^2=0.97 P^b<0.001		
(13) log FY=0.973 log TP+0.391 log $\bar{z}$−0.016 log TDS−1.377 R^2=0.92 P^b<0.001		
(14) FY=0.071 TP+0.165 $\bar{z}$−1.164 R^2=0.96 P^b<0.001		
(15) log FY=0.967 log TP+0.384 log $\bar{z}$−1.390 R^2=0.92 P^b<0.001		
(16) FY=0.092 TDS−0.006 $\bar{z}$−1.148 R^2=0.62 P^b<0.001		
(17) log FY=0.826 log TDS−0.241 log $\bar{z}$−1.224 R^2=0.405 P^b<0.001		

[a] t-test.
[b] F-test.

did not significantly reduce the predictive efficiency of the model (R^2 = 0.96; Table 2), but deletion of the total phosphorus variable substantially reduced the predictive power of the model (R^2 = 0.62) and eliminated the contribution of the mean depth term. This supports our hypothesis that much of the univariate predictive power of total dissolved

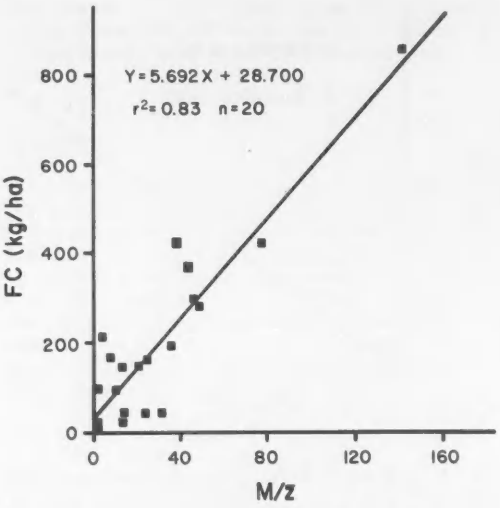

FIG. 3. Regression of fish standing crop (FC) on macrobenthos biomass (kg/ha)/mean depth (m) ($M/\bar{z}$).

TABLE 3. Regression equations, based on data set 3, for estimating fish biomass (FC in kg/ha) from lake surface area (Ao in ha), mean depth ($\bar{z}$ in m), and macrobenthos standing crop (M in kg/ha) for 20 lakes and ponds.

Simple regressions	r^2	P[a]
(1) FC=5.692 $M/\bar{z}$+28.700	0.83	<0.001
(2) log FC=0.76 log $M/\bar{z}$+1.116	0.58	<0.001
(3) FC=1.918 M+67.610	0.20	<0.050
(4) log FC=0.737 log M+0.793	0.28	<0.015
(5) FC=−5.868 $\bar{z}$+231.708	0.05	<0.325
(6) log FC=−0.720 log $\bar{z}$+2.382	0.27	<0.020
(7) FC=0.004 Ao+193.441	0.01	<0.669
(8) log FC=−0.064 log Ao+2.103	0.04	<0.421
Multiple regressions		
(9) FC=5.674 $M/\bar{z}$+0.002 Ao+27.738	R^2=0.83	P[b]<0.001
(10) log FC=0.762 log $M/\bar{z}$−0.0009 log Ao+1.114	R^2=0.58	P[b]<0.001
(11) FC=2.437 M−10.270 $\bar{z}$+87.262	R^2=0.35	P[b]<0.025
(12) log FC=0.769 log M−0.753 log $\bar{z}$+1.098	R^2=0.58	P[b]<0.001

[a] t-test.
[b] F-test.

solids was due to cross correlation with the total phosphorus concentration.

FISH BIOMASS

Macrobenthos biomass/mean depth was the best univariate predictor (r^2 = 0.83; Fig. 3) in data set 3 (Table 3). Macrobenthos biomass alone explained only 20% of the observed variation in fish biomass. Mean depth and lake surface area were not significantly correlated with fish biomass (Table 3). Logarithmic transformations yielded a weak relationship between mean depth and fish biomass (r^2 = 0.27). No cross correlation was found between variables. Multivariate models yielded no improvement in predictive power (Table 3).

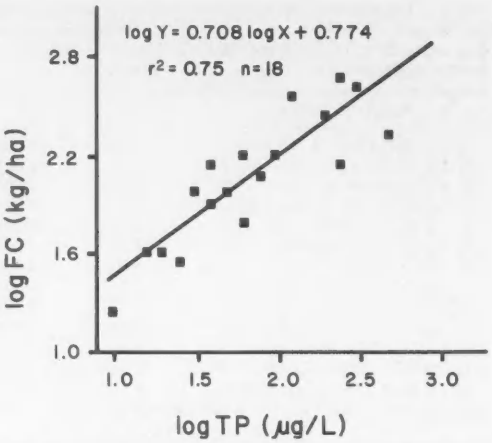

FIG. 4. Regression of fish standing crop (FC) on total phosphorus concentration (TP).

Log-transformed total phosphorus was the best estimator of fish yield in data set 4 (log FC = 0.708 log TP + 0.774; r^2 = 0.75; t-test, $P < 0.001$; Fig. 4). The linear model explained less than half the variance of the logarithmic form (FC = 0.593 TP + 98.520; r^2 = 0.35; t-test, $P < 0.010$).

Discussion

Total phosphorus concentration and macrobenthos standing crop/mean depth were superior to total dissolved solids, mean depth, and the morphoedaphic index as predictors of fish yield when comparisons were based on the same data set. Total phosphorus concentration may be a better predictor of fish yield than macrobenthos biomass/mean depth, but no objective conclusion regarding their relative powers can be drawn until both indices are compared for the same data set. The data required for such a comparison has not been published, but should be developed because, from a practical standpoint, it is easier to obtain estimates of average total phosphorus concentration. The relationship between fish yield and total phosphorus is very similar in form and identical in predictive power (r^2 = 0.84) to Oglesby's (1977b) relationship between fish yield and phytoplankton standing crop. This similarity is to be expected given the demonstrated dependence of phytoplankton biomass on phosphorus availability (Schindler 1975).

Simple models for predicting fish yield are likely to be specific for the climatic zone from whence the data set originates. Schlesinger and Regier (1982) have already demonstrated this effect on MEI. The long-term fish yield of Lake Nipissing, Ontario (not included in the preceding analysis), predicted from the total phosphorus models, corresponds closely to the observed yield, but the predicted yields for two tropical lakes are far below the observed values (Table 4). This discrepancy probably arises because of the much higher

TABLE 4. Predicted fish yield (PFY in kg/ha) compared to reported fish yield (FY) for three lakes based on multivariate (A, Eq. (14), Table 2) and simple (B, Eq. (1), Table 2), models. Total phosphorus (TP in μg/L) and mean depth ($\bar{z}$ in m) were the variables used.

Lake	$\bar{z}$	TP	FY	A PFY	B PFY
Nipissing, Ontario[a]	4.6	37	2.9	2.2	3.4
George, Uganda[b]	2.4	200[d]	138.4	13.4	15.2
Naivasha, Kenya[c]	4.7	48[c]	25.3	3.0	4.3

[a]Anthony and Jorgensen 1977.
[b]Burgis and Dunn 1978.
[c]Litterick et al. 1979.
[d]Ganf 1974.
[e]J. Kalff, McGill University, personal communication.

TABLE 5. Reported fish standing crops (FC in kg/ha) compared to fish standing crops (PFC) predicted from the average total phosphorus concentration (TP in μg/L) for five Tennessee Valley reservoirs.[a]

Reservoir	TP	FC	PFC (linear)	% FC
Kentucky	270	280	259	92.5
Cherokee	160	230	193	83.9
Norris	20	150	110	73.3
Nottley	50	143	128	85.5
Douglas	110	125	164	131.2

[a]Taylor (1971).

fish production in tropical lakes where the fish exhibit continuous growth and year-round reproduction which shortens generation times. Furthermore, in tropical lakes most of the commercially important fish species are herbivores. This results in a more efficient transfer of the energy fixed by photosynthesis to the fish biomass (Fryer and Iles 1972; Litterick et al. 1979).

Problems of inadequate reporting of fish catch, differing accessibility of lakes to the fishermen, and variation in fishing effort with lake size, between years, and with the differing market value of the fish species (Jenkins and Morais 1971; Adams and Olver 1977; Matlock 1971) yield a significant and uncontrollable source of variation in attempts to predict fish yield. Given these constraints it is unlikely that the predictive power of single or multivariate indices of fish yield will improve greatly in the near future.

Total phosphorus concentration and macrobenthos biomass/mean depth were also the best estimators of fish biomass in lakes. Although we cannot conclude which of these two variables is the better predictor of fish biomass, it is easier to measure total phosphorus concentration. Furthermore, in reservoirs the macrobenthos standing crop is severely reduced by water level fluctuations, oxygen depletion, and heavy siltation which alters the major route of energy transfer from benthos to zooplankton (Cowell and Hudson 1967; Isom 1971; Nagiec 1977).

The linear form of the total phosphorus model developed for lakes yielded estimates of fish biomass for five Tennessee Valley Authority reservoirs that were 73–131% of the fish biomass measured by rotenone poisoning (Table 5). Although the number of tests is small, these data suggest that total phosphorus concentration may have considerable potential as a predictor of fish standing crop in reservoirs as well as in lakes.This might be expected, a priori, because phosphorus is the primary regulator of phytoplankton growth and standing crop (Schindler 1975; Wetzel 1975; Oglesby 1977a). Zooplankton and macrobenthos standing crop are also positively correlated with total phosphorus (Hall et al. 1970; Dermott et al. 1977). Additional work in this area appears warranted.

The power of the macrobenthos biomass/mean depth predictor of fish biomass in lakes may derive from the fact that, functionally, it incorporates the importance of allochthonous materials which are a major energy source for invertebrates in the food chains of smaller lakes (Rau 1980), and from the fact that benthos is the major pathway of energy transfer in lakes (Wissmar and Wetzel 1978; Jonasson 1978). The generality of this model which is based on estimates of total fish biomass and includes lakes in a diverse lake set containing very different fish communities and incorporating lakes over a broad geographic range (0–56°N) implies a near-constant energy transfer from benthos to fish regardless of the number or type of fish species present. We hypothesize that individual species expand their diet to include previously unexploited food types when interspecific competition is reduced thereby maintaining a constant biomass irrespective of species numbers. This hypothesis is currently under study.

We believe the negative relationship between mean depth and fish biomass and yield occurs because in shallow lakes the littoral zone occupies a larger percentage of the total bottom area and because critical nutrients are recycled more rapidly there. Carignan and Kalff (1980) have shown that aquatic macrophytes obtain nearly all of their phosphorus requirements from the littoral sediments. In addition, 50% of the observed flux of dissolved total phosphorus to the pelagic zone results from the decay of these macrophytes (Carpenter 1980). The littoral zone has the highest level of primary productivity (Efford 1967; Welch and Kalff 1974); greater zooplankton abundance and biomass (Straskraba 1965; Jonasson1978); greater macrobenthos diversity, biomass, and turnover rates (Moore 1950; Anderson and Hooper 1956; Jonasson 1978); and greater fish abundance and biomass (Werner et al. 1977; Keast et al. 1978). It is also becoming evident that there is a direct proportionality between biomass of various trophic levels (Nakashima and Leggett 1975; Gascon and Leggett 1977). It is understandable then, that when comparing waters of similar nutrient status, lakes with a greater portion of the bottom area as littoral zone have higher fish productivity (Scott et al.1938; Ryder et al. 1974; Wilson et al. 1975).

Total dissolved solids have been widely used as an estimator of fish harvest and biomass because of their relative ease of measurement and the presumption that total dissolved solids were proportional to the essential elements such as phosphorus and nitrogen. Despite the fact that elemental proportions in water appear to vary as a result of the geochemistry of the watershed and with the addition of agricultural and sewage pollution (Ryder et al. 1974; Dillon and Kirchner 1975; Oglesby 1977a), we found this variable was significantly correlated with total phosphorus concentration and macrobenthos biomass. Although a poor estimator of fish yield when used alone, total dissolved solids contributed sig-

nificantly to the variance explained by multivariate models.

The best known index of fish yield, the morphoedaphic index, originally proposed as a fish yield estimator in north-temperate lakes (Ryder 1965), consistently performed poorly when compared with other available indices using a common unconstrained data set. The greatest contribution of the morphoedaphic index has been its demonstration that empirical prediction of fish yield was possible. This has led to the development of several indices based on phytoplankton standing crop, macrobenthos standing crop, and total phosphorus concentration (Oglesby 1977b; Matuszek 1978; this study) which appear to be superior in terms of their generality, predictive power, and the insights they give into the nature of the biological processes operating. When properly constrained (lakes of similar water quality, geographic area, average depth, etc.) the MEI does, however, have acceptable predictive power (Ryder et al. 1974; Jenkins 1977; Matuszek 1978; Schlesinger and Regier 1982). More research is required to determine which index will prove most useful as a general, unconstrained predictor of fish yield. Given the key role of phosphorus in the production dynamics of freshwater ecosystems, the strong predictive relationships we report here, and their relative ease of measurement, we suggest that future research might be profitably directed towards a more in-depth examination of the relationship between phosphorus levels in lakes and fish biomass and yield.

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Use of Cycle Dummy Variables and Race Escapement in the Fraser River Sockeye Salmon (*Oncorhynchus nerka*) Recruitment Function

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GARDNER, P. N. 1982. Use of cycle dummy variables and race escapement in the Fraser River sockeye salmon (*Oncorhynchus nerka*) recruitment function. Can. J. Fish. Aquat. Sci. 39: 264 – 269.

The recruitment function for the Fraser River sockeye salmon (*Oncorhynchus nerka*) stock was estimated by allowing cycle differences between year-classes to be represented by dummy variables, by allowing the effects of weight on cycle year differences to be included through the use of biomass forms of the variables, and by disaggregating year-class escapement by race according to freshwater lake residence to represent differences between races. Comparisons were made with the conventional model.

Key words: year-class cycle dummies, biomass variables, race escapements, sockeye salmon

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La fonction recrutement dans le stock de saumons nerka (*Oncorhynchus nerka*) du fleuve Fraser a été estimé de la façon suivante: en représentant par des variables simulées les différences de cycle entre classes d'âge; en incluant, par le biais des variables biomasse les effets du poids sur ces différences de cycle; et enfin, en séparant la survie des classes d'âge d'après le temps de résidence en eau douce de façon à refléter les différences entre races. Nous comparons avec le modèle conventionnel.

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THIS paper reports on some modifications used to improve the estimates of a salmon recruitment function. These estimates were to be used in a fisheries management program which required a high level of confidence to be placed in their predictive power. It is usual in salmon studies, with observations available for escapement and catch, to use a metered model such as a Ricker recruitment function. There are also a number of nonlinear programs available which will directly minimize the sum of the squared residuals (Patterson 1978) without introducing the bias involved in linearizing nonlinear functional forms. Nevertheless, if we can assume that the distribution of the error is log-normal (Ricker 1973, p. 337), then the Ricker recruitment function can be classified as intrinsically linear (nonlinear with respect to the variables and linear with respect to the parameters (Kmenta 1971, p. 451–458)) and no bias will result. Models such as these provide useful "interpolations" only, however, and cannot be said to be estimators of biological parameters for the underlying population (Chapman 1973, p. 328).

The problem with even very sophisticated "interpolations" is that they work well in hindsight but are sometimes poor when foresight is required for management purposes. Ideally, the recruitment function should take into account all environmental, interspecific, intraspecific, and harvesting effects. However, reliable data simply do not exist to develop such a model.

Alternatively, the basic data can be disaggregated to allow the influence of one or more characteristics of the stocks to be picked up in the parameter estimates. The Fraser River sockeye salmon (*Oncorhynchus nerka*) spawn in 44 creeks and streams of the Fraser River watershed. As soon as the spawn hatch, they migrate to 11 freshwater lake systems connected with those creeks and streams. It is assumed that these lake systems act as the major racial distinction for sockeye.

After spending two winters in those lakes and streams the salmon migrate to oceanic feeding grounds and return after two winters. About 90% of the returnees are 4-yr-olds; the presence of 3- and 5-yr-olds is insignificant. Therefore, it was assumed that a four-year-class characterizes each cycle. Researchers have disaggregated by cycle year for some time but with limited success.

There are five species of salmon available to the nets of fishermen in the fishery through which the Fraser River sockeye salmon migrate; it is thus a multispecies fishery. The Fraser River watershed acts as a host to sockeye and pink salmon (*Oncorhynchus gorbuscha*) only, and as the peaks of the spawning cycles for pink and sockeye do not overlap too seriously every 2nd year and only partially in other years, the multispecies problem has been ignored.

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The Model and the Data

The basic Ricker function (Ricker 1975) used in many salmon studies is

(1) $R = aE(\exp(-bE))$

where R = recruitment (lagged 4 yr), a, b = parameters, exp = exponential operator, E = escapement.

The first modification is the inclusion of a depensation parameter (Dahlberg 1973) to give

(2) $R = aE^d(\exp(-bE))$

where d = depensation parameter.

This expression is usually transformed into a linear estimator by taking natural logs:

(3) $\ln(R/(E^d)) = \ln a - bE.$

(It is assumed that the error is multiplicative.) There are three problems associated with this conventional form of estimator. First, the dependent variable R is modified by the independent variable E. In addition to the empirical problems which result from having linear and monotonic transformations of the same variable appear on both sides of the equation, another problem is that if the variance of E is larger than the variance of R, it will tend to dominate the ratio in the estimation. Finally, the depensation parameter d must be estimated by some iterative technique requiring changes in the value of "d" over a specified range.

These problems can be alleviated by introducing a second modification to the basic Ricker model by rearranging expression (3) to give:

(4) $\ln R = \ln a + bE + d(\ln E).$

This modified form of the Ricker recruitment model needs observations on R and E to estimate the parameters a, b, and d. Data on escapement of sockeye are available from the International Pacific Salmon Fisheries Commission (IPSFC) for the 44 creeks and streams feeding into the 11 major lake systems in the Fraser River watershed (IPSFC 1937–75). These data are based on actual counts of fish swimming in the spawning streams.

Data on catch are available for sockeye entering the fishing gauntlet prior to ascending the Fraser River to spawn (IPSFC 1937–75). Catch is not available by race, however. Fraser sockeye caught in waters outside those designated as treaty waters by the Sockeye Salmon Fisheries Convention are not included in the IPSFC catch totals which had to be revised to include nontreaty catch (D. Anderson, Fisheries—Pacific Region, 1090 West Pender St., Vancouver, B.C., unpublished nontreaty catch). These revised catch totals include sockeye taken off the west coast of Vancouver Island, and those caught by U.S. and Canadian fishermen in the IPSFC convention area, by Canadian fishermen in Johnstone Strait, and by Canadian Native Indians from the sockeye escaping up the Fraser River. Recruitment was assumed equal to the sum of escapement and catch.[1]

[1]All these data are available in machine readable form from the Program in Natural Resource Economics at the University of British Columbia.

There are the usual measurement errors; however, the greatest source of error is that escapement observations are for net escapement and not gross escapement, i.e. the count is not of the numbers escaping fishermen's nets but of numbers reaching the spawning grounds. Mortality in the upstream migration can vary from 5% to as much as 60%. Thus true recruitment is not given by summing net escapement and catch. However, counts on the spawning grounds do give a more accurate figure for the number of spawners involved in the formation of the next year-class, and net escapement can be partially adjusted by including the Indian catch which takes place after the salmon escape the commercial fishery. (The IPSFC estimates of Indian catch (IPSFC 1944, p. 65–74) date back only to 1941. Foerster's estimates of Indian catch (1968, p. 58) are used for 1938, 1939, and 1940.)

Foerster (1968) has emphasized the importance of average weight for the success of upstream migration and year-class survival rates. If fish are too large they cannot swim through shallow areas and if they are too small they cannot survive the ordeal of ascending difficult waterways. Weight data are available (IPSFC 1937–75) and can provide information on the parameter estimation process. Ricker (1973) has suggested that the relationship between recruitment and escapement is most likely to be log-normal. Although the use of weight to act as a proxy for upstream mortality does not involve this recruitment–escapement relationship directly, it was assumed that weight would modify the variables in a multiplicative way (biomass as well as numbers of fish) and not in an additive way (average weight).

There is a second, more compelling reason to use weight in a multiplicative form. One consequence of using the modified form of Ricker recruitment function in expression (4) is that multicolinearity is likely to be high between E and its monotonic transformation, $\ln E$. This can be reduced by using instrumental variable, WE, in place of either of the E's. "WE" is simply escapement multiplied by the average cycle weight of sockeye and is thus a nonmonotonic transformation of E.

The third modification to the basic Ricker recruitment function involves the inclusion of weight in a multiplicative form as an explanatory variable. It is usual to put recruitment in terms of numbers of fish, but for management purposes the value of the harvest is optimized and the biomass form of recruitment is more useful, i.e. reproduction of biomass is more important than reproduction of numbers. For this reason, the recruitment variable was also modified by weight to put it in biomass form.

Another potential source of error is the blockage of the Hell's Gate section of the Fraser. The fishways were completed and used by the spawners in 1945 (IPSFC 1946, p. 5). Subsequent counts indicated that these fishways led to an average 100% increase in escapement to spawning grounds above Hell's Gate. This once-and-for-all change in escapement should not affect estimation too seriously because the figures on escapement had been "in situ" counts on spawning beds, and escapement would be the net of the effects of the Hell's Gate obstruction. However, actual recruitment includes gross escapement, and subsequent figures would include the increased net escapement both in calculated recruitment totals and in escapement totals. This presents no problem for escapement, but does reflect the measurement error associated with using net rather than gross recruitment.

It was assumed that the observations would be for a different range of the escapement–recruitment function and no corrections were made to the data.

The sockeye fishery is based on a prolific stock with a large production surplus and the stock is subjected to great variability in the environment. As a result, recruitment does fluctuate, but it appears to do so in a cyclical fashion and only to a limited extent. The 2nd and 4th years of the cycle are about the same size, twice as large as the recruitment for the 3rd cycle year, but only half the size of the recruitment for the 1st cycle year.

Because the parent stock dies after spawning, a change in escapement level leads to equilibrium within one 4-yr cycle. This should preclude any problems associated with disequilibrium and it was assumed that the sockeye stock had reached equilibrium by 1938. As there is only one year-class for each cycle and all four year-classes were assumed independent, there were no stock structure problems associated with alterations in the year-class array within a given stock.

Because of the limited success encountered in disaggregating the data by cycle year, a fourth modification was introduced which involved the use of cycle dummies to mark the cycle year and yet leave the data in pooled form. Keeping the data pooled in one estimator is statistically more desirable than disaggregating by cycle year. It was assumed that the introduction of dummy variables in slope and intercept form would allow for differences in parameters among the four year-class cycles (Kmenta 1971, p. 419–423). Dummies in intercept form permit a qualitative difference in the intercept among the four year-classes and dummies in slope form permit qualitative differences among the slope coefficients for the four year-classes.

The fifth modification to the basic model was the disaggregation of escapement by race.

Estimation Results

The estimation process was divided into two stages. In the first, each of the five modifications was tested for significance compared with a conventional model. As all five modifications contributed a significant improvement in fit, the second stage of estimation used all five modifications simultaneously.

Table 1 gives the results for the first two modifications. As one would expect, releasing the constraint on the depensation parameter in expression (3) (it was assumed equal to unity) does improve the fit in expression (4) (depensation parameter is 1.02). All the tests were run with an intercept ($\ln a$), but the intercept values are not included in the first four tables.

Because of the significant improvement encountered with modifications one and two, expression (4) was retained as the basic model for comparison to test for the significance of further modifications.

Modification three involved the use of biomass forms of the variables in place of the numbers (Table 2). The most significant results were obtained with

$$(5)\quad \ln WR = \ln a + bE + \mathrm{d}(\ln WE)$$

where WR = biomass recruitment (weight times numbers), WE = biomass escapement (weight times numbers). Note that the biomass form of recruitment was more significant than the numbers form and that biomass escapement was more significant in log form.

TABLE 1. A comparison between the conventional Ricker recruitment function (expression (3)) and a rearrangement (expression (4)) which permits depensation to be estimated. Coefficients, "t" statistics, and R^2 corrected for degrees of freedom are in Tables 1–5, and intercept values are omitted in Tables 1–4.

Expression	Coeff. for E	"t" stat. for E	Coeff. for $\ln E$	"t" stat. for $\ln E$	R^2
(3)	−0.39	−4.56			0.38
(4)	−0.41	−2.11	1.02	4.9	0.59

TABLE 2. A comparison between the rearranged Ricker recruitment function using numbers of fish (expression (4)) and the same function using biomass for recruitment and the log of escapement (expression (5)).

Expression	Coeff. for E	"t" stat. for E	Coeff. for $\ln E$ or $\ln WE$	"t" stat. for $\ln E$ or $\ln WE$	R^2
(4)	−0.41	−2.11	1.02	4.9	0.59
(5)	−0.42	−2.26	1.05	5.3	0.64

For the fourth modification, expression (4) was tested using dummy variables to mark the year-class cycles. Dummy sequences in both slope and intercept form with 2-yr (every other year, i.e. 1 0 1 0), 4-yr (once every 4 yr, i.e. 1 0 0 0), 2/2-yr (2 good followed by 2 bad years, i.e. 1 1 0 0), and 8-yr cycles were used.

As an alternative way of picking cycles, a polynomial distributed lag was used with lengths of lag varying from 2 to 8 yr (Kmenta 1971, p. 492–495). This technique implies that the cycle is some function of conditions in the environment in previous years and assumes that the weights on the previous escapements follow a polynomial of a specified degree, i.e. past conditions have an increasing then decreasing impact on future survival and growth rather than just a steadily declining influence. The sockeye recruitment hypothesis does not supply any a priori specifications for the degree (increasing and decreasing impacts) and length (number of years the influence is felt) of the polynomial and an iterative approach was used to allow the data to determine the most statistically significant results using the R-squared delete technique. As the results were not as significant using distributed lags as they were with cycle dummies in slope and intercept form, the latter were used instead of the former.

Expression (6) gives the form of cycle dummy which gave the best fit:

$$(6)\quad \ln R = \ln a + bE + d_1 \ln E_1 + d_2 \ln E_2 + d_3 \ln E_3 + d_4 \ln E_4$$

Intercept dummies did not appear to be significant; however, dummy forms of the log of escapement were significant in a 4-yr cycle (Table 3). Note that the compensatory parameter "b" in expression (4) is indeed negative in (6) and that the depensatory parameter "d" in expression (4) is positive in (6). The expression in (6) implies that recruitment is directly related to cycle year escapement with depensatory coefficients distinguished by year-class. To offset this effect, recruitment is inversely related (through the exponential oper-

TABLE 3. A comparison between the rearranged Ricker recruitment function (expression (4)), the same function with slope cycle dummies (expression (6)), and the same function disaggregated by cycle year-class (expression (4)).

Expression dummies and cycle years	Coeff. for E	"t" stat. for E	Coeff. for ln$E$	"t" stat. for ln$E$	R^2
(4)	−0.41	−2.11	1.02	4.9	0.59
(6)	−0.7	−3.8			0.68
DUM:1			0.8	6.5	
DUM:2			0.7	5.7	
DUM:3			0.682	5.6	
DUM:4			0.694	5.9	
(4):1	−0.8	−0.9	1.03	1.8	0.01
(4):2	−0.17	−0.3	0.86	2.4	0.79
(4):3	3.6	0.8	−2.0	−0.7	0.07
(4):4	−2.3	−2.2	−2.3	−1.8	0.51

TABLE 4. A comparison between the rearranged Ricker recruitment function (expression (4)) and the same function using log of total escapement and escapement disaggregated by race (expression (4) disaggregated by race, see expression (7) for race descriptions).

Expression and race	Coeff. for E	"t" stat. for E	Coeff. for ln$E$	"t" stat. for ln$E$	R^2
(4)	−0.41	−2.11	1.02	4.9	0.59
(4)			1.24	6.2	0.66
ELF	−6.3	−1.9			
EST	−0.6	−3.3			
EC	−1.4	−3.2			
ES	−1.6	−3.0			

ator) to escapement; however, the compensatory coefficient is not sensitive to the year-class cycle.

Using cycle dummies in slope form appears to lead to a significant improvement. For purposes of comparison the results for regressions based on data disaggregated by cycle year (an alternative conventional model) are also given in Table 3. Note that even though the corrected R is high for disaggregated cycle 2, neither of the coefficients is significant at either $P \gtrsim 0.025$ or 0.01. The reason is that there are only 6 degrees of freedom for the disaggregated regression whereas there are 28 for the pooled data regression.

Modification five involved the disaggregation of the escapement data by race. The best results are given in Table 4. Only four of the eleven races (see below) were significant (if the intercept is dropped, ELF becomes significant at the 0.025 level), but their inclusion in place of total escapement leads to a significant improvement.

In the second stage of testing, all five modifications were included in the estimation process. Both the compensatory and the depensatory parameters were tried in cycle form using cycle lengths of 2, 4, 2/2, and 8 yr. All 11 races were tested again and some of the race escapement variables were not statistically significant every year, but became significant in dummy form for specific years only. A test was performed using the "F" statistic (Kmenta 1971, p. 373–374) to check on the possibility of changes in parameter values over the 34 yr under observation. The results indicate that basic parameter values have not changed significantly over the whole period. The best version of the estimator is given in expression (7); (the parameter coefficients have been deleted for brevity and clarity and all escapement figures not in log form have been scaled down by dividing by one million). The key to the 11 race escapements is also given with the freshwater residence lakes in parentheses (note that not all races were significant). Results of the estimation are given in Table 5.

TABLE 5. A comparison between the rearranged Ricker recruitment function (expression (4)), and the same function using biomass recruitment, an intercept plus one intercept dummy, the log of biomass escapement, and escapement disaggregated by race in both numbers and biomass form with year-class cycle distinguished by slope dummies (see expression (7) for race descriptions). Intercept values are inserted (as INTER, DUM3 etc.) in the coefficient and "t" statistic columns for E.

Expression and race	Coeff. for E	"t" stat. for E	Coeff. for ln$E$ or lnWE	"t" stat. for ln$E$ or lnWE	R^2
(4)	−0.41	−2.11	1.02	4.9	0.59
(7)			1.34	14.0	0.97
INTER	−2.3	−1.7			
DUM3	0.65	3.6			
ELF	51.9	5.6			
EH	−50.0	−4.3			
EST	−2.8	−7.9			
EC	−3.1	−10.3			
*W*EQ	−4.7	−4.3			
EN	9.5	4.7			
ENE	37.6	4.1			
ELF2	−58.8	−6.0			
ELF3	−80.9	−7.4			
*W*EH1	5.3	2.9			
EST1	9.8	5.7			
*W*EST1	−1.3	−5.1			
EST3	118.3	4.8			
*W*ENT1	70.2	6.8			
*W*EC1	4.7	5.8			
*W*EQ1	−657.9	−6.4			
*W*EQ2	2314.5	7.4			
EQ4	26.1	4.2			
*W*EN1	−5.9	−7.3			
*W*ES2	−5.9	−10.6			
*W*ES3	−3.8	−5.0			
*W*ES4	−0.9	−8.7			

(7) $\ln WR = \text{INTER} + \text{DUM3} + \ln WE + \text{ELF} + \text{EH} + \text{EST} + \text{EC} + WEQ + \text{EN} + \text{ENE} + \text{ELF2} + \text{ELF3} + WEH1 + \text{EST1} + WEST1 + \text{EST3} + WENT1 + WEC1 + WEQ1 + WEQ2 + \text{EQ4} + WEN1 + WES2 + WES3 + WES4$

where WR = biomass recruitment in pounds of fish; INTER = intercept; DUM3 = intercept dummy for cycle year 3; WE = biomass escapement in pounds of fish; prefix W = the variable is in biomass form; suffix 1, 2, 3, 4 = the variable is in dummy cycle form with the weight in the 1st, 2nd, 3rd or 4th yr of the cycle; ELF = Lower Fraser (Pitt); EH = Harrison (Harrison); ELC = Lillooet, Fraser Canyon (Nahatlatch); ESA = Seton–Anderson (Seton and Anderson); EST = South Thompson (Shuswap and Adams); ENT = North Thompson; EC = Chilcotin (Chilko); EQ =

Quesnel (Quesnel); EN = Nechako (Francois and Fraser); ES = Stuart (Takla, Trembleur, Stuart); and ENE = Northeast (Bowron).

It is interesting to note that in expression (6), where aggregate escapement data were used, the cycle year-class form is most significant for the depensatory parameter, whereas in expression (7) where escapement is disaggregated by race, the cycle year-class form is most significant for the compensatory parameter.

According to the IPSFC (1965, p. 3), to avoid changing the cyclic character of the Fraser River sockeye salmon stock, "escapements are controlled to fit the historical pattern of productivity in each of the four cycle years. A large escapement is provided in the year of the dominant run, a reduced number of fish in the year of sub-dominant run and lesser numbers of fish are permitted to escape under normal circumstances in the two 'off-years'." The justification for this policy is that consistent size of escapement would tend to interfere with the predator, food, and prey relations and lead to cycles of a different sequence. This means that escapement regulation, which was initiated in 1946, has not offset the natural cycles and lends support to the use of cycle dummies to act as a proxy for external influences.

The significance of the year-class cycle dummies indicates that the major influence on recruitment is the escapement 4 yr earlier. It is likely, however, that the effect of disturbances does carry over into other year-class cycles. The experience with distributed lags tends to support this and indicates that the greater the number of periods between disturbances, the smaller the covariance. An iterative technique was used to estimate the coefficient of correlation (Kmenta 1971, p. 287–289) in expression (7); a test for autoregression based on the estimated coefficient of correlation indicated significant first-order autocorrelation.

It is possible to use the estimated correlation coefficient to adjust the parameter estimates, but this approach was not used. The most important reason for not adjusting the parameters is the fact that the relation among year-classes in both the freshwater and oceanic areas is so complex (Foerster 1968) that no simple autoregressive scheme is likely to account for what is probably some unexplained systematic influence on recruitment. Secondly, it is not clear just what effect the use of cycle dummies would have on estimation of a correlation coefficient. Even if the estimation were valid, it may be that the autoregressive scheme should be of the fourth order rather than the first. Finally, the use of parameter estimates adjusted for a coefficient of correlation different from zero would make the optimal escapement problem exceedingly complex in a management model.

Race escapements which were not significant either in full or cycle year form were ELC and ESA. ESA is the smallest race escapement and it is easy to understand why it is not significant. ELC is a medium-sized escapement but demonstrates virtually no cycle differences in escapement totals. Perhaps this absence of a cyclical element explains its lack of significance. For the remaining race escapements the cycle year form usually marks years of abnormally large or small escapements for that race. Note that for some races the biomass form is more significant than numbers. This is particularly true for the 1st cycle year which is a year of abnormally large escapement for many races. As the IPSFC uses time of entry models to facilitate control of escapement by race, it appears that disaggregating escapement data by race is a feasible method to estimate parameter values for a management model.

One rather disturbing feature is the degree of correlation between EST1 and *W*EST1. The variables are not monotonic transformations of each other, but the correlation is understandably high as the variables are in cycle form (fewer observations) and differ only by the weight factor.

To avoid multicolinearity the R-squared delete technique was used (with Standard Error of Regression, SER, substituted for R-squared); in all other cases of variable correlation, elimination of one of the variables within a pair did not increase SER significantly. However for EST1 and *W*EST1, any attempt to eliminate one of the variables led to a very significant decrease in explanatory power for the regression. Note that the coefficients bear different signs: perhaps the relationship between biomass and numbers plays an important role in migration survival for this area.

Conclusions

This study supports previous findings that recruitment is sensitive to racial differences, average weight, and year-class cycle in sockeye salmon stocks. These factors appear to influence fertility, survival, and growth in a highly significant manner.

The standard error of the regression was very low for expression (7), and it would be hard to achieve a closer fit using more sophisticated statistical techniques including nonlinear estimation. The use of qualitative differences in the form of weight, race, and cycle year-class allows the regression process to change the slope coefficients for the recruitment function each year in a 4-yr cycle. In a sense these coefficients have been derived from a type of nonlinear estimation process in which discontinuous changes are permitted during any 4-yr cycle. For some purposes it may be better to have a smooth nonlinear function. However, the closeness of fit and the stability of the coefficients over a 34-yr period appear to show that changes in weight, race, and year-class within a 4-yr cycle can act as proxy variables for environmental changes which may not have been picked up by a smooth and continuous nonlinear function. It is hoped that the qualitative nature of these parameter estimates will allow managers to use qualitative data to improve forecasting in the future. Nevertheless, it is important to remember that despite these modifications, the recruitment function in expression (7) still provides an "interpolation" only.

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Juvenile Salmon Residency in a Marsh Area of the Fraser River Estuary

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Large numbers of juvenile chinook salmon (*Oncorhynchus tshawytscha*), chum salmon (*O. keta*), and pink salmon (*O. gorbuscha*) were present within tidal channels of a marsh area in the Fraser Estuary between March and June 1978. The tidal channels investigated dewatered at low tide, necessitating daily emigrations by juvenile salmon out of the channels. While pink fry emigrated from tidal channels at the early and middle stages of ebbing tides, most chum and chinook fry emigrated near the later stages of ebbing tides. Mark–recapture studies demonstrated that chinook and chum fry resided temporarily in the marsh prior to migrating into the Pacific Ocean and returned to the same channel on several tidal cycles. Pink fry were abundant in the channels, but appeared to be transient. Chinook and chum showed an increase in average length which was attributable to estuarine growth.

Key words: chinook salmon, chum salmon, pink salmon, juvenile residency, marsh tidal channel, Fraser Estuary, estuary growth

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Entre mars et juin 1978, il y avait un grand nombre de jeunes saumons chinook (*Oncorhynchus tschawytscha*), keta (*O. keta*) et roses (*O. gorbuscha*) dans des chenaux de marée des régions marécageuses de l'estuaire du fleuve Fraser. L'eau des chenaux de marée étudiées se retirant à marée basse, les jeunes saumons étaient forcés à émigrer quotidiennement hors de ces chenaux. Alors que les alevins de saumon rose quittaient les chenaux de marée au début ou au milieu du reflux, la plupart des alevins de saumons keta et chinook émigraient vers la fin du reflux. Des expériences de marquage et de recapture démontrèrent que les alevins de saumons chinook et keta résidaient temporairement dans la région marécageuse avant d'émigrer dans l'océan Pacifique et retournaient au même chenal pendant plusieurs cycles de marée. Les alevins de saumon rose étaient abondants dans les chenaux, mais semblaient n'y être que de passage. On a observé chez les saumons chinook et keta une augmentation de la longueur moyenne attribuable, semble-t-il, à la croissance estuarienne.

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ESTUARIES serve as nursery areas for the larvae and juveniles of commercially and recreationally important finfish and shellfish (Smith et al. 1966; Lauff 1967; Haedrich and Hall 1976). For anadromous species, estuaries can provide a transition zone wherein both juveniles and adults gradually adapt to environmental differences between freshwater and marine environments. Anadromous Pacific salmon (genus *Oncorhynchus*) are extremely abundant on both coasts of the North Pacific Ocean, and billions of juvenile salmon annually pass through estuaries on the Asian and North American Pacific coasts.

The Fraser River system in British Columbia supports some of the world's largest runs of Pacific salmon (Northcote 1974). Juveniles of two species of salmon, chum (*Oncorhynchus keta*) and chinook (*O. tshawytscha*), occur in the Fraser Estuary between March and July (Dunford 1975; Anon. 1978; Levy et al. 1979). Much of the original marsh area in the Fraser Estuary has been lost from dyking and subsequent development (Forrester et al. 1975). There is concern (Dorcey et al. 1978) that historical and present developments in the estuary have had negative impacts on Fraser salmon runs.

Information on the residency behavior of juveniles is required to evaluate the importance to salmon of Fraser and other marsh habitats. Both chum (Mason 1974; Healey 1979) and chinook salmon juveniles (Reimers 1973; Healey 1980) live temporarily in some estuarine areas along the Pacific coast prior to moving into the coastal marine environment. Species that are resident in estuaries for an extended period are potentially more sensitive to losses and changes in estuarine habitats than forms which utilize these areas merely for migratory passage. The prime objective of this study was to establish the relative length of residency by juvenile salmon in a major marsh of the Fraser estuary.

Materials and Methods

The study area was on Woodward Island (49°6′N, 123°8′W) within the Ladner marsh–island complex of the

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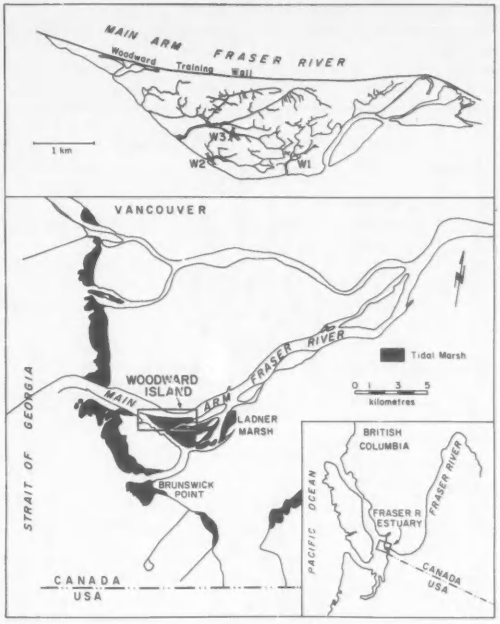

FIG. 1. Location of sampling sites in tidal channels on Woodward Island within the Fraser River Estuary.

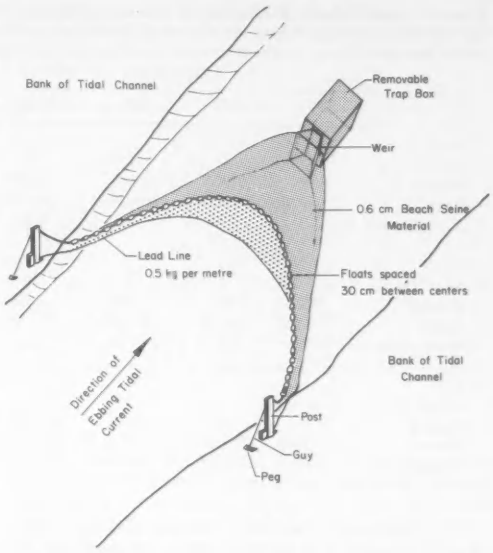

FIG. 2. Intertidal trap net designed to sample fish utilizing tidal channels on Woodward Island.

Fraser River Estuary (Fig. 1). Woodward Island is an intertidal marsh of ~128 ha and has a plant community dominated by the sedge, *Carex lyngbyei* (Kistritz and Yesaki 1979). As a result of variation in Fraser River discharge (commonly approaching 8 000 $m^3 s^{-1}$ in peak freshet periods between May and July, but falling to 700 $m^3 s^{-1}$ in winter months), marsh areas in the vicinity of Woodward Island are dominated by freshwater or by brackish water at different times of the year (Kistritz 1978). Highest salinities on Woodward Island (10‰) occur during low Fraser River flows in winter months. During March–July 1978, the period of investigation, salinities on Woodward Island ranged between 3‰ in March and 0‰ during the latter 4 mo (Westwater Research Centre, unpublished data).

Three tidal channels on Woodward Island (Fig. 1) served as sampling sites. Tidal channels are dendritic waterways which extend into, and drain, marsh areas. They may be up to several hundred metres in length, tapering from a mouth several to tens of metres wide into narrow terminal branches, often less than 1 m in width. Other predominant fish habitats surrounding Woodward Island are referred to as sloughs (Dunford 1975) and encompass a subtidal habitat immediately adjacent to marsh areas. Slough habitats are open-ended, exposed to the flow of the Fraser River at all tide levels. Because tidal channels undergo dewatering on low tides, fish move out of the channels and into sloughs as the tide ebbs, and reenter the tidal channels on a successive flood tide.

A large beach seine was used as an intertidal trap (Cain and Dean 1976) to capture fish utilizing tidal channels. The trap net (0.6-cm mesh, 2.4 m deep) was stretched across a tidal channel at a high slack tide, preceding a steep tidal drop, and fastened to stakes set into the bank of the channel (Fig. 2). As the tide ebbed, most of the fish population in the channel upstream from the trap net either entered the trap or was retained in a small pool behind the net. When the channel was nearly dewatered, all the fish that had not entered the trap were concentrated into a small section of the net, and together with those from the trap, transferred into a 20-L cooler. The catch was either kept alive in 64-L plastic pails until enumerated or else immediately preserved in a 10% Formalin solution.

The removable trap box (Fig. 2) permitted investigation of the timing of fish emigrations from tidal channels on ebbing tides. The trap box was emptied hourly. After the tide had dropped to a level where about a 0.5-m depth of water remained in a pool of the tidal channel immediately upstream from the trap net, the net was pursed and the fish in front of the net were captured.

To mark juvenile salmon for mark–recapture studies, fine fluorescent grit was applied with an air gun at 5.6 kg/cm^2 pressure (Healey et al. 1976). Fish were held in a pen for 1 d prior to being marked. About 200 fish were placed on a 3-mm plastic mesh screen rack (25 × 40 cm) and then into a bath of MS-222 anesthetic. Once the fish were motionless, the rack was placed on a table and the grit sprayed from a distance of about 40 cm. The racks containing the fish were then rinsed to get rid of excess grit, and the fish allowed to recover in oxygenated 64-L pails. Groups of fish were marked with different colors of fluorescent grit so that several release groups were distinguishable. Marked fish were held for 1 d prior to being released, as it was during the initial period after marking that mortality was thought to occur (Healey et al. 1976).

TABLE 1. Gear efficiency of intertidal fish traps for capturing juvenile salmon in three tidal channels on Woodward Island during 1978.

	Sampling site			
	W1	W2	W3	All sites
Chinook				
No. of tests	2	3	2	7
Average	46%	68%	70%	62%
Range	25–66%	50–74%	60–79%	25–79%
Scaling factor	2.17	1.47	1.43	1.61
Chum				
No. of tests	2	4	2	8
Average	37%	44%	55%	45%
Range	12–62%	28–59%	14–66%	12–66%
Scaling factor	2.70	2.27	1.82	2.22
Pink				
No. of tests	2	2	1	5
Average	37%	42%	86%	49%
Range	19–54%	26–48%	—	19–86%
Scaling factor	2.70	2.38	1.16	2.05

To recover marked individuals, fish were checked for fluorescent grit marks by inspection under an ultraviolet (uv) light source. About 50 live fish were first placed on 3-mm mesh racks (identical with the marking racks) in an anesthetic (MS-222) bath. As soon as the fish were motionless, the rack was lifted out of the bath and passed under the uv light. Both sides of the fish were inspected for marks by flipping the rack over onto an identical rack and passing it under the uv light a second time.

Two types of mark–recapture studies were conducted: gear efficiency assessments and residency determinations. Gear efficiency assessments (Kjelson and Colby 1977) were designed to determine the proportion of the fish population in the tidal channel that was sampled by the gear used. After setting the nets and waiting for the tide to recede to the tops of the sedge plants lining the channel banks, a known number (~100) of marked fish of a given species was introduced into the tidal channel about 200 m upstream from the traps. Recovery rates of marked fish were used to estimate gear efficiency factors (the inverse of the average recovery rates) and to scale the catch data to corrected density data. Estimates of the areas of the tidal channels upstream from the sampling sites (W1 = 4227 m^2, W2 = 24 192 m^2, W3 = 6745 m^2) were obtained by planimetry off Fraser River Delta Series Maps 72-24T (Department of Lands, Forests, and Water Resources, Government of British Columbia) and used to express the fish catch data on an areal basis.

Gear efficiency assessments were conducted with juvenile chinook, chum, and pink salmon (*O. gorbuscha*) in three tidal channels (W1–W3) between April and June 1978 (Table 1). Recaptures of marked chinook, chum, and pink fry were lowest in W1; consequently, scaling factors were highest at this site. There were consistent species differences in recapture rates. Chinook fry recaptures were higher than pink and chum fry recaptures during gear efficiency assessments, the one exception being a higher recapture rate of one group of marked pink fry in W3 (Table 1). On average, 62% of the marked chinook fry but only 45 and 49% of the marked chum and pink fry were recaptured during gear efficiency estimates. Leakage of fish around the traps, stranding of fish in pools upstream of the sampling site, and selective predation on marked fish may have affected the gear efficiency of the intertidal trap nets.

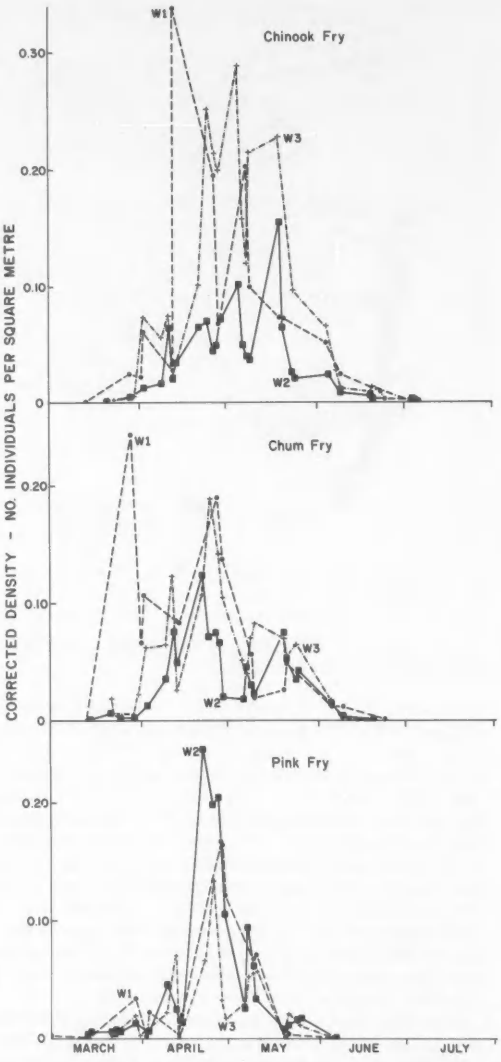

FIG. 3. Density of juvenile salmon in three Woodward Island tidal channels (W1–W3) during 1978. All numbers adjusted for gear efficiency (see Table 1) and tidal channel area.

Three short-term mark–recapture studies were designed to measure residency of young salmon in the study areas. Groups of marked fish were released into tidal channel W2 on three occasions during May 1978. Between 1 and 7 d

TABLE 2. Results of mark–recapture studies on juvenile salmon conducted on Woodward Island during 1978.

Date of release	Stage of tide	Release period (d)	Recapture date	Species	No. released at W2	No. recaps. in W1	No. recaps. in W2	No. recaps. in W3	Total No. recaps.	[a]Scaled % recap.
May 7	Flood	1	May 8	Chinook	697	6	249	10	265	56
				Chum	238	—	40	2	42	40
				Pink	401	2	2	—	4	2
May 21	Flood	2	May 23	Chinook	351		17	3	20	8
				Chum	193	Not	5	1	6	7
				Pink	50	done	4	—	4	19
May 12	Ebb	7	May 19	Chinook	625	—	43	20	63	15
				Chum	171	—	3	—	3	4
				Pink	262	—	—	—	—	—

[a] $\left\{\left[\sum_{i=1}^{n} (\text{No. recaps. in tidal channel } (i) \times \text{gear efficiency scaling factor in tidal channel } (i))\right] / \text{Total no. marks released at W2}\right\}$ where n is the number of tidal channels sampled.

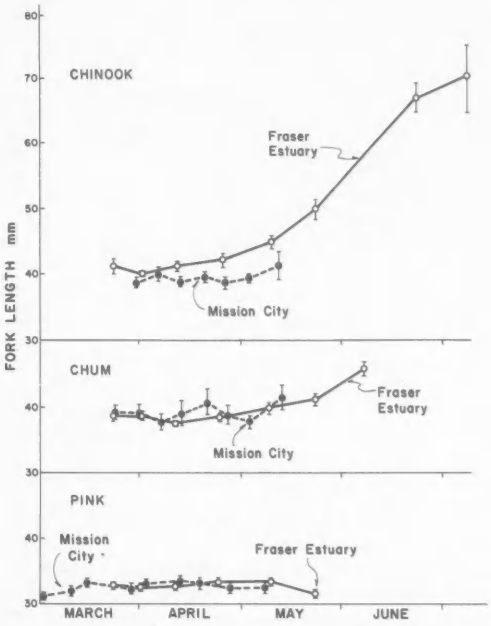

FIG. 4. Seasonal change in average juvenile salmon fork length ± 95% confidence limits during 1978 at W1 on Woodward Island (Fraser River Estuary) and at Mission City, B.C., 100 km upstream from the Fraser Estuary.

after the release of marked fish, the tidal channels were sampled and the fish inspected for marks. Additional marked fish were recovered when fish caught in subsequent sampling operations were inspected under uv light.

Results

Corrected density data for chinook, chum, and pink salmon (Fig. 3) illustrate the seasonal pattern of juvenile salmon occurrence in Woodward Island tidal channels. Between March and May, juvenile chinook, chum and pink salmon were numerically dominant in the tidal channel fish community on Woodward Island (Levy et al. 1979). Juvenile coho salmon (*O. kisutch*) (yearling smolts) and juvenile sockeye salmon (*O. nerka*) (underyearling fry and yearling smolts) also occurred in the tidal channels, but in relatively low numbers. The most abundant salmonid (juvenile chinook) reached an average density of 0.18 individuals per square metre in early May (Fig. 3). The other two abundant salmonids, pink and chum, reached average densities of 0.16 and 0.14 individuals per square metre, respectively, in late April.

Recaptures of marked salmon fry (Table 2) provided evidence for temporary residency and for different residency times of pink, chum, and chinook fry in the vicinity of Woodward Island. Most of the recaptured fish were chinook fry (Table 2). Relatively few pink fry were recaptured, with the exception of four marked individuals following the May 21–23 release. Chum fry recapture rates (scaled percent) were intermediate between those for pink and chinook fry. Recaptures of marked fry during routine sampling operations that followed these studies indicated that chinook fry had a relatively long residence in the marsh. Virtually all incidental recaptures of marked fish were chinook fry. Recoveries of marked fish from the May 12 release group, in addition to the May 19 recaptures shown in Table 2, occurred on the following sampling dates:

	May 20	May 23	May 24	June 6
W1	—	Not sampled	Not sampled	—
W2	5 chinook	1 chum	—	1 chinook
W3	5 chinook	3 chinook	1 chinook	—

Recoveries of marked fish from the May 21 release group, in addition to the May 23 recaptures (Table 2), also occurred on June 19 (one chinook fry in W3) and June 20 (one chinook fry in W3). The longest recorded residence times for marked chinook, chum, and pink fry were 30, 11, and 2 d, respectively.

Preserved fry were measured to the nearest 0.1-mm fork-length and compared with those obtained in a 4 × 4 floating fry trap (Conlin and Tutty 1979) which was operated by the Department of Fisheries and Oceans, Vancouver, B.C., between early March and late May 1978 at Mission City, B.C., 100 km upstream of the Fraser Estuary. There is evidence for growth of juvenile chum and chinook salmon in the Fraser Estuary (Fig. 4). The chum and chinook fry samples from Mission City ranged between 37.5–40.9 mm and 38.2–39.4 mm in average fork length, respectively, during March–May. Chum and chinook fry obtained on Woodward Island were similar in length to those at Mission City until early May and thereafter increased in size reaching average lengths of 46.2 mm for chum in early June and 70.5 mm for chinook during early July. Pink fry trapped on Woodward Island were similar in fork length to specimens obtained at Mission City throughout their occurrence in the marsh (Fig. 4) and did not increase in length during this period.

The emigration sequence of juvenile salmon from tidal channels was studied on four sampling dates. Consistent patterns of movement of pink, chum, and chinook fry were observed. Pink salmon was the first species to emigrate from the tidal channel during its dewatering phase (Fig. 5). Large numbers were caught during the middle draining period 2 and 3 h after high tide. Very few juvenile chum and chinook salmon were caught during ebbing tides; most were captured near the end of the dewatering phase of the channel at low tide. Similar patterns of emigration were observed throughout April and May 1978.

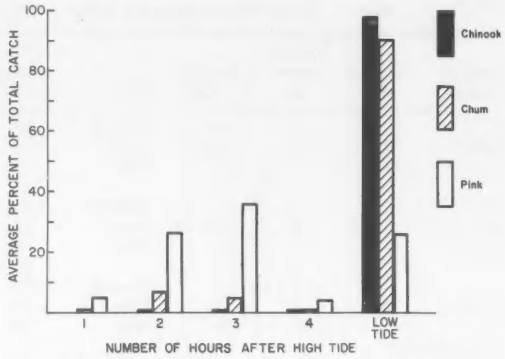

FIG. 5. Percentage of juvenile salmon in trap catches between high and low tide in W3 averaged for four sampling dates during May of 1978.

Discussion

The anadromous progeny of Fraser salmon must pass through the lower Fraser River and estuary at some point during their juvenile existence. Results from this study provide the first evidence that two species of juvenile salmon, chum and chinook can reside in Fraser Estuary marshes prior to entering the marine environment. Chinook was the species which resided in Woodward Island tidal channels for the longest period during May 1978. During mark–recapture experiments, the recapture frequencies probably underestimated the number of marked chinook fry resident on Woodward Island. Only three tidal channels were sampled (representing about 25% of the total tidal channel area on Woodward Island), providing a limited opportunity to recapture marked individuals. Recaptures of marked fry indicated that chinook are capable of month-long residency periods in the vicinity of Woodward Island.

Our results suggest that the increase in average fork length demonstrated by the estuary chinook population represents estuarine growth. The habit of juvenile chinook salmon to remain in tidal channels during the early stages of the ebbing tide probably represents a mechanism for maintaining a position close to the mouths of tidal channels at low tide and avoiding being flushed downstream by tidal and river currents. This behavior allows resident fry to feed on the rich crustacean and insect food resources of the marsh tidal channels (Levy and Northcote 1981) and is conducive to estuarine growth. The largest chinook fry captured on Woodward Island were close to 70 mm in fork length by July, also indicating long marsh residency. Similar observations have been made in the Nanaimo Estuary (Healey 1980) where it was estimated that individual chinooks spent an average of 25 d rearing and emigrated after reaching a fork length of 70 mm.

In contrast with the resident chinook fry, pink fry in Woodward Island tidal channels were transient and only a few were recaptured during mark–recapture studies. The length data indicate no increase in mean size between March and May. Juvenile chum salmon demonstrated a tidal channel residence of intermediate duration between that of pink and chinook fry. A slight increase in mean size was realized by the population and a number of marked chum fry were recaptured during mark–recapture studies. Juvenile chum residency times in the Nanaimo Estuary varied between 0 and 18 d during two field seasons of mark–recapture studies in 1975 and 1976 (Healey 1979).

Although juvenile chinook salmon are relatively less abundant than pink or chum (by an order of magnitude) as downstream migrants in the Lower Fraser River (Department of Fisheries and Oceans, Vancouver, B.C., unpublished data), because of their strong tendency to reside in estuary marsh habitats, they in fact reach higher densities in tidal channels than do the other two species. In late April and early May 1978, the maximum corrected density of chinook, chum, and pink fry in Woodward Island tidal channels was 0.18, 0.14, and 0.16 individuals/m^2, respectively (average values for the three tidal channels sampled). The tendency for chinooks to reside in the tidal channels for a relatively long period resulted in this species concentrating on Woodward Island and becoming the predominant salmonid in the marsh. Pink and chum fry, although much more abundant at Mission City, reared in the marsh for relatively short periods and were not concentrated in the tidal channels of Woodward Island to the same extent as chinook fry.

A difference in the degree to which marshes are utilized as rearing habitats by juveniles may contribute to segregation of the five species of *Oncorhynchus* present in the Fraser River system. Although millions of adult sockeye salmon annually spawn in the Fraser River system, most sockeye fry utilize lakes as juvenile rearing areas (Northcote 1974), and only few are present in tidal channel marsh habitats. The progeny of

Fraser coho spawners mostly use streams as juvenile rearing habitats and are only occasionally captured in marsh tidal channels. Pink fry, although abundant in the tidal channels in even-numbered years, migrate quickly through the marsh and into the Strait of Georgia. The two species that overlap in the marsh to the greatest extent are chum and chinook. This overlap is reduced through differences in migration timing, with chum preceding chinook in the marsh, and through different marsh residency periods, with chum spending a relatively short time in the marsh, when compared with chinook.

Along the Pacific coast of North America, chinook salmon range from the Ventura River in California north to the Chukchi Sea in Alaska, and major spawning populations of chinook salmon occur in large Pacific rivers and their tributaries (Mason 1965). Juvenile chinook have been found in the following large river estuaries: the Sacramento River Delta (Kjelson et al. 1981), the Columbia River Estuary (Johnsen and Sims 1973), the Fraser River Estuary (this study), and the Skeena River Estuary (Hoos 1975). Additionally, estuarine rearing of juvenile chinook salmon has been documented in two relatively small coastal river systems including the Sixes River Estuary, Oregon (Reimers 1973), and the Nanaimo River Estuary, B.C. (Healey 1980). Other chinook rivers having well-developed marshes and/or estuaries likely support populations of resident chinook juveniles in the estuary for part of the year.

The utilization of rearing habitats both in freshwater (Tutty and Yole 1978) and in the estuary can benefit specific chinook runs. The habit of juveniles to concentrate and rear in estuaries, as well as in river tributaries, serves to extend the area of available juvenile rearing habitat. Estuary characteristics of high productivity and intermediate salinity (Odum 1971) may promote the survival of estuary residents. Furthermore, the chinook that rear in freshwater may benefit from reduced competition for space and food resources, if indeed these are limiting, by having a component of the population emigrate to the estuary soon after emergence from the gravel. The overall productivity of a chinook population (number of smolts entering the marine environment) is probably higher for river systems having well-developed estuaries with marshes which serve as additional juvenile rearing areas than in systems without such a habitat.

Scale analysis of adult Sixes River (Oregon) chinook salmon enabled Reimers (1973) to quantify the contribution of five different chinook life history types to the adult population for the 1965 brood year. The most common type was chinook which had remained in freshwater for about 3 mo, and then reared in the Sixes River Estuary for an additional 3 mo. Approximately 90% of the successfully returning adults showed estuarine circuli in the 1st year of scale growth. Some stocks of Fraser River chum and especially chinook salmon may well realize a similar enhancement of survival following a period of juvenile residency in the marshes of the Fraser Estuary.

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Preliminary Evaluation of a Method to Determine the Age of Sablefish (*Anoplopoma fimbria*)

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BEAMISH, R. J., AND D. E. CHILTON. 1982. Preliminary evaluation of a method to determine the age of sablefish (*Anoplopoma fimbria*). Can. J. Fish. Aquat. Sci. 39: 277–287.

Age of sablefish (*Anoplopoma fimbria*) was estimated using broken and burnt otoliths. A partial validation of the method was achieved using fish of known age, oxytetracycline-injected fish, and results of tagging studies. Estimated ages indicated that most sablefish stocks contain a large number of fish that are much older than previously determined using the scale method of age determination. This new information on the age and growth of sablefish indicates that strategies for the management of the sablefish fishery should be re-evaluated.

Key words: sablefish, age determination, age and growth, otoliths, age validation, fisheries management

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Nous avons estimé l'âge de morues charbonnières à l'aide d'otolithes sectionnés et brûlés. Il a été possible de vérifier partiellement la validité de cette méthode en utilisant des poissons d'âge connu, des poissons injectés à l'oxytétracycline et les résultats d'expériences de marquage. D'après ces estimations, la plupart des stocks de morues charbonnières renferment un grand nombre de poissons beaucoup plus âgés qu'on ne l'avait cru en se fondant sur les déterminations d'âge par les écailles. Il faudrait donc, à la suite de cette information nouvelle sur l'âge et la croissance de la morue charbonnière, réévaluer les stratégies de gestion de pêche de cette espèce.

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SABLEFISH or blackcod (*Anoplopoma fimbria*) is an important commercial species found in the Pacific Ocean off the coast of North America from northern Mexico to the Bering Sea and off the Asian coast from Kamchatka to the northeastern coast of Japan. The center of abundance appears to be in the northeastern Pacific between Vancouver Island and the Shumagin Islands.

Sablefish have been fished commercially by North Americans since the late 1800s (Ketchen and Forrester 1954), but it was not until Japanese fishermen entered the fishery in the early 1960s that stocks were subjected to intensive exploitation. In waters off the Canadian coast, early Japanese fishing (1968–76) occurred outside of Canada's fishery jurisdiction (beyond the 12-mile territorial limit), and as the domestic fishery was minimal there was little Canadian interest in developing a management strategy. After extension of fisheries jurisdiction to 200 miles in 1977, Canada assumed responsibility for management of sablefish. By then, participation by the foreign fishery had become intensive and participation by Canadian fishermen was increasing.

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As part of the program to develop management strategies, it was essential that the age composition of the stocks be determined. There were only a few previous reports of age and growth of sablefish, and most of these studies used scales for the identification of annuli (Pruter 1954; Heyamoto 1962; Shubnikov 1963; Kodolov 1967, 1976; Kennedy and Pletcher 1968; Webb and Lockner 1973). Results, though never validated, suggested that sablefish is a relatively fast-growing, short-lived species, yet the results of recent tagging studies (Beamish et al. 1978, 1979, 1980) indicated that the annual growth of mature fish may be very small. More generally, there has been mounting support for the view that ages estimated from scales may not be reliable for long-lived species whose rates of growth become greatly reduced after attainment of maturity at a relatively young age (Aass 1972; Beamish 1973; Mills and Beamish 1980; Harrison and Hadley 1979).

This report describes preliminary results of studies designed to develop a reliable method of age determination for sablefish. Scales, sections of fin rays, and otoliths were examined to determine which structure exhibited the clearest pattern of growth zone formation. At the same time, experiments were initiated to verify that zones identified as annuli actually

formed once a year. Because the results to date suggest that previous estimates of age are seriously in error and that consequences of this error to the management of sablefish are equally serious, we feel it is advisable to produce a report before the validation studies are completed in 5–10 years.

Materials and Methods

Otoliths, fin rays, and scales were collected, stored, and processed as described by Beamish and Chilton (1977) and Beamish (1979). Collections of juvenile sablefish were obtained for length frequency measurements from research cruises and from commercial trawl fishermen. Samples of submarket-sized juveniles obtained from commercial fishermen could be biased because of codend mesh size selection. However, samples obtained during research cruises were caught by nets having a 2.5-cm-stretched-mesh codend liner and were considered to be unbiased.

As part of another study to identify stock units and to monitor growth of sablefish, large numbers (98 900) of juvenile and adult sablefish captured in traps and trawls were tagged and released. A portion of the adult fish captured in traps was given an intraperitoneal injection of oxytetracycline to produce a "time" mark in the otolith. The procedures used for capture and tagging of sablefish and the injection of the oxytetracycline have been described in Beamish et al. (1978, 1979, 1980). When tagged fish were recovered, they were remeasured and otoliths were removed and stored in 50% glycerin in darkened containers.

In 1972, Kennedy and Smith (1972) tagged 1003 juvenile sablefish captured with baited barbless hooks. Some of these fish were recovered and sampled in 1979, 1980, and 1981 by Canadian observers on foreign and domestic fishing vessels or when returned by Canadian fishermen.

United States scientists, involved in a tagging study of sablefish that started in 1973, permitted us to use otoliths collected from these fish in 1979 and 1980 to validate the aging method. These fish were caught in the Canadian zone and sampled for length, sex, and otoliths at sea or returned whole for sampling on shore. Ages were determined from otoliths without any prior knowledge about the fish except the capture date. Age at tagging was estimated by comparing the length at tagging with the age–length relationship derived in this report.

As most of the tagged fish were retrieved from frozen commercial catches, it was necessary to examine the change in size that occurs when sablefish are frozen and then thawed. A sample of 50 freshly caught sablefish was selected, to represent a wide range of sizes, and killed with anesthetic (MS 222). These fish were then measured for length and weight, tagged, and frozen at sea. After 7 days the specimens were brought back to the laboratory, thawed, and remeasured.

An estimate of routine measurement error was made by comparing measurements before and after tagging. During tagging procedures, lengths were customarily recorded before applying the tag, and the recorder routinely requested a second length measurement be made for about every 10th fish after tagging. A comparison of a series of 100 consecutive duplicate measurements from one cruise is included in this report.

Results

A comparison of ages determined from scales and from the method recommended was not made. The alternating pattern of closely and widely spaced circuli was rarely observed and annuli (the zone of closely spaced circuli) as identified by Pruter (1954) were rarely observed beyond the first few years. Circuli were closely spaced, broken, and formed irregularly. There also was a high percentage of regenerated scales. Because of the general absence of any recognizable pattern, other structures were examined.

Sections of all fin rays and fin spines were unsatisfactory for age determination because growth zones were difficult to find. When zones could be detected only a few could be identified in fish that from their size had to be more than a few years old. Many fin rays had evidence of some form of internal bone resorption similar to the resorbing of bone that occurs in lingcod fin rays (Beamish and Chilton 1977). Fins were also very oily when dried and difficult to process.

Of the three structures examined, otoliths provided the best pattern of continuous growth zones. The pattern of growth on the external surface of the otolith was readily identified for the first few zones, just as with scales, but subsequent zones were poorly defined and obscured by irregularities in the growth pattern. A more distinct growth pattern was observed when the otolith was broken dorsoventrally through the nucleus and the exposed surface was burnt and painted with cedar wood oil (Christensen 1964). Thin sections of otoliths (Beamish 1979) were also examined, but the pattern of growth could not be identified as readily as from the broken and burnt surface. Therefore, the broken and burnt surface of the transverse section through the nucleus of the otolith was selected for estimating the age of sablefish. The annulus was defined as the translucent zone or the zone of slower growth.

Method of Age Determination

Burnt sections in Fig. 1B–E are of better-than-average quality and clearly show a pattern of alternating growth zones. The annulus which appears as a dark zone when photographed using reflected light is readily visible in most sections.

The first few annuli are usually difficult to identify because of the relatively rapid otolith growth and the indistinct annuli. In clearer sections (Fig. 1B) there are more definite changes in the first few growth zones that result in the formation of rather broad translucent zones. While these zones frequently contain numerous, narrow, opaque zones or checks, they do not obscure the annulus. However, in many sections (Fig. 1C), the first few annuli are not obvious except as ridges that appear on the edge of the transverse section. The position of the first two to three annuli can be identified because the width of the annual growth zones during the first few years is quite large compared to widths of zones laid down in subsequent years. This relatively rapid growth is even more apparent from the otolith surface (Fig. 1A). The relatively large amount of otolith growth in the first few years suggests that the growth of the fish also is quite rapid. An examination of the length frequencies of samples of sablefish (Fig. 2A) confirmed that fish growth in length is quite rapid and that the first annulus forms well outside of the center of the otolith

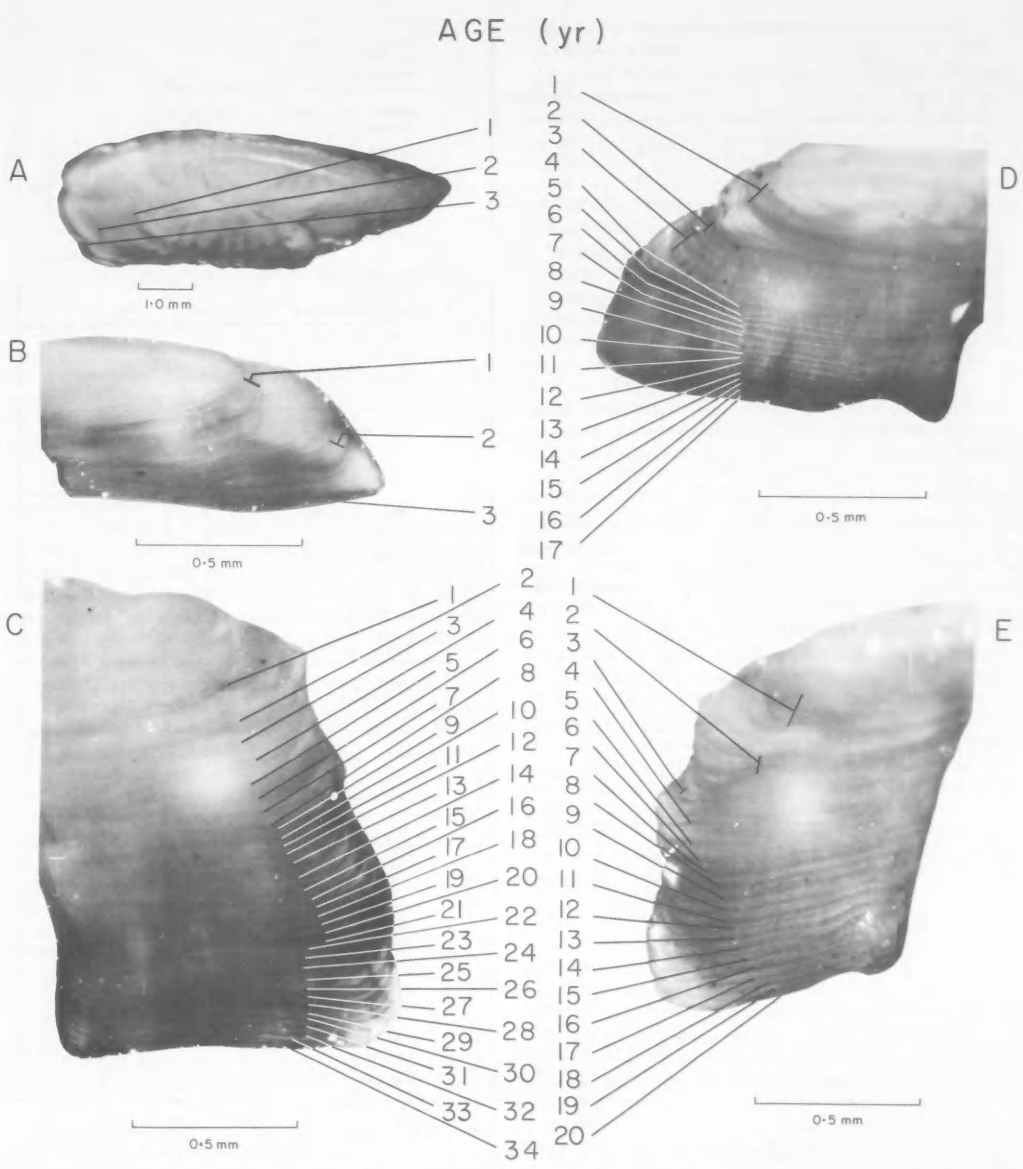


FIG. 1. (A) Surface of an otolith from a juvenile male sablefish 49 cm, age 3, sampled in May. The highlighting in some areas of the annulus is a result of the lighting used for the photograph. (B) Section of the above otolith. Note that annuli are difficult to identify but that ridges appear in the outline of the section at the approximate position of each annulus as observed in 1A. (C) Example of an average section of a very old sablefish, 77-cm female, age ~34 yr, sampled in May. (D) Example of a slow-growing old fish; 51-cm male, age 17 yr, sampled in May. (E) Example of an easily aged, fast-growing sablefish, 96-cm female, age 20, sampled in May.

(Fig. 1A, B). In many fish the relative positions of the first three annuli are similar and a comparison of the thickness of an otolith from a 3-yr-old fish with the otolith of unknown age will indicate the approximate location of the third annulus. As fish age, the pattern of alternating growth zones becomes more distinct and concentrated on the interior of the otolith.

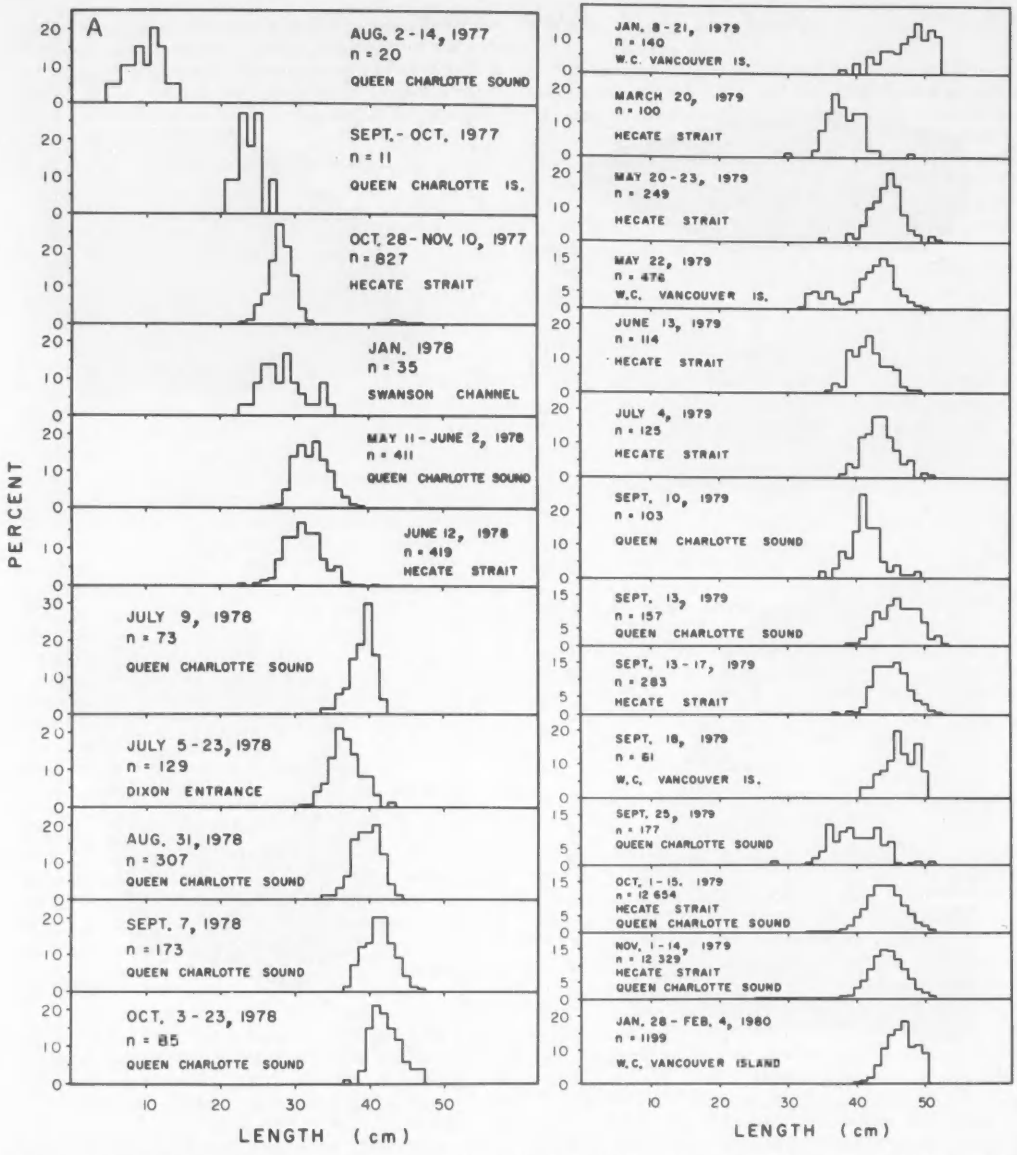


FIG. 2. (A) Length frequencies of total or random samples of juveniles of the 1977 year-class obtained off the west coast of Canada from August 1977 until February 1980.

Checks within the opaque zone were identified by their narrow width and the tendency to be present in only a portion of the opaque zone, i.e. they rarely formed a continuous zone (Fig. 3A). Checks that form in the vicinity of the third annulus sometimes are sufficiently distinct to make the identification of the fourth annulus difficult (Fig. 1D). However, the last check of the rather broad annulus of the third zone can be quite faint, while the fourth and subsequent annuli are more distinct. This change in annulus formation occurs at about the same time changes were observed in the length frequency distribution of juveniles (Fig. 2A, B). The prominence of checks varied among samples.

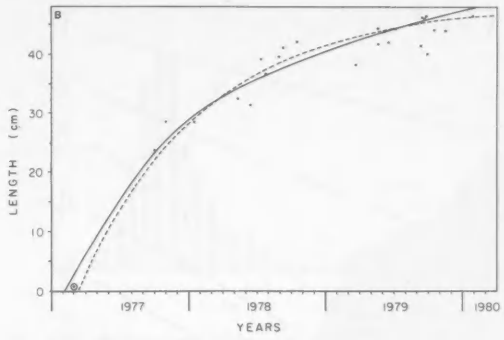


FIG. 2. (B) A von Bertalanffy growth curve (broken line) and a growth curve fitted by eye (solid line) for the mean sizes of each of the frequency distributions in Fig. 2A. Length at time zero was estimated to be 1 cm.

Few otoliths have a pattern of alternating growth zones as prominent as those in Fig. 1D and E. While the thickness of the zones after age 3 is quite different in these two otoliths, the annuli form in a regular pattern and are not obscured by checks. It is noteworthy that the fish represented by Fig. 1D and E were both about the same age, yet one was a slow-growing male and the other was a fast-growing female indicating that size of the fish or the thickness of the otolith after age 3 or 4 is not necessarily an indicator of age.

Figure 1C is about average in clarity and while the photograph is more difficult to interpret than the actual section, it is apparent that some annuli are difficult to identify because of the absence of prominent growth zones or because of the presence of checks within the annual pattern of growth. In most individuals these checks tend to be less apparent as the fish ages; however, in some individuals they dominate a portion or all of the pattern of zone formation making the recognition of annuli extremely difficult. As most otoliths from older fish contained some areas where annuli were difficult to interpret, there was usually some doubt about the accuracy of the age determination. Despite this problem it appeared that the pattern of alternating translucent and opaque zones observed on the broken and burnt otoliths occurred annually. It remained to be demonstrated that the translucent zone identified as an annulus did form once a year for all age-classes in the population.

VALIDATION OF METHOD

When validating a method of age determination, it is essential that it be proven reliable for all or most age-classes in a population and not just for the first few years of comparatively rapid growth. Traditional techniques using length frequency analysis or the examination of the edge of the otolith section are not satisfactory for older, slower-growing fishes.

In this study tagged fish were used to validate the method. Even though a sufficient number of fish have not been recovered to demonstrate conclusively that the growth zones identified as annuli do form once a year, the preliminary results do indicate that the method is probably valid for all age-classes.

VALIDATION WITH KNOWN AGE FISH

A partial validation of the method was possible when otoliths were collected from a small sample of "known age" sablefish. The juvenile sablefish tagged in 1972 by Kennedy and Smith (1972) had an average length of 38 cm (Fig. 4). A comparison of the length frequency of these fish with the length frequencies obtained for the 1977 year-class from 1977 to 1980 (Fig. 2A, B) indicates that most of the fish tagged in Kennedy's study were age 1+.

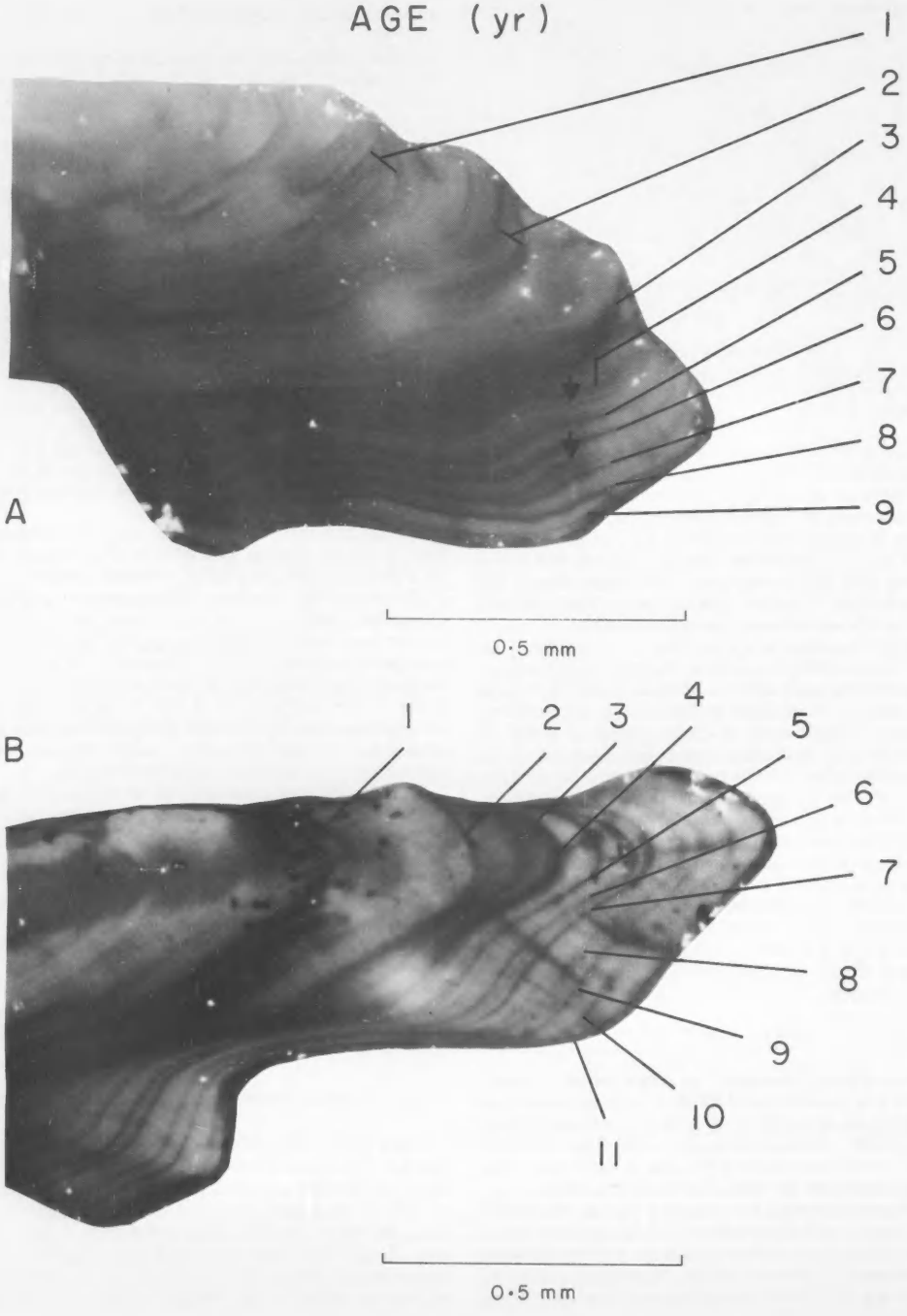
Two fish which were 38 cm and 42 cm when tagged were recovered in the commercial fishery in 1979 and measured 62 cm (male) and 68 cm (unknown sex). Unfortunately no otoliths were obtained. By June 1980, four more of these fish were recaptured and otoliths were obtained from a 60-cm male, a 63-cm male, a 64-cm female, and a 68-cm male. As these fish ranged from 34 to 37 cm when tagged and were probably age 1+ in 1972, they would be 9 or 9+ depending on whether or not the new year's growth was visible in mid-1980. Ages were determined initially without the readers knowing the history of the specimens and were 8+, 9+, 8+, and 10 yr. When the reader was informed of the history of the fish, a second determination resulted in ages of 9, 9, 9+, and 10.

The annuli in two of the otoliths were very difficult to identify and the sections were difficult to photograph; thus only the best section from the four otoliths is shown in Fig. 3. The section (Fig. 3A) shows a definite pattern of alternating opaque and translucent zones. As discussed, the positions of the first three annuli are difficult to identify. The approximate position of the 3rd annulus can be identified by comparing the thickness of the section with the thickness of the age-3 section in Fig. 1. The last five annuli in Fig. 3A are quite clear and a comparison of the thickness and pattern of these zones with some of the older sections in Fig. 1 clearly shows that older fish simply have added more zones to the otolith.

In April 1981, two additional fish were recovered. Both fish were females that were 34 and 38 cm when tagged in August 1972, and 72 and 77 cm, respectively, when recovered in April 1981. There is little doubt that these fish would be 1+ when tagged and therefore would be 10 or 10+ yr old when recovered. Otoliths from both fish were aged without any knowledge of the fish except the month of sampling, and both fish were aged as 11 yr. A photograph of the otolith section from one of these fish (Fig. 3B) does not show the annual growth zones as clearly as they can be seen using a microscope. After knowing that this fish (Fig. 3B) probably was age 10 yr, the reader felt that the third annulus was not a true annulus.

VALIDATION FROM OXYTETRACYCLINE INJECTIONS

During 1979, 53 tagged fish were recovered that had been injected with oxytetracycline (OTC) and released in the fall of 1977, and 307 were recovered that had been similarly treated in 1978. Not all otoliths from these fish have been examined, but some form of an OTC mark was present on those that have. The OTC mark was visible on the interior surface when viewed in cross section while occasionally being absent from the exterior surface of the otolith. Because most fish had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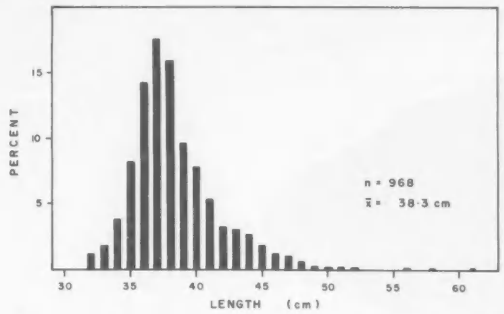


FIG. 4. Length frequency of the sablefish tagged off the northeast coast of Vancouver Island in the summer of 1972 by Kennedy and Smith (1972).

grown very little during the release period, the mark was frequently near the edge of the otolith. A few fish such as a 62-m male, marked and released off the west coast of Vancouver Island in September 1977 and recovered September 1979 at a length of 69 cm and an age of 7+ yr, did show that two opaque and two translucent zones had formed in the 2 years prior to recapture. Another 53-cm male, released in September 1977 off the west coast of Vancouver Island and recovered at a length of 53 cm in September 1979, was aged as 16 yr when recaptured, and while no apparent change in length occurred, two closely spaced opaque zones could be identified as having formed after the OTC mark was deposited.

In 1980, a total of 39 fish were recovered that had been injected with OTC when tagged in 1977 and 1978. In all cases, the OTC mark was visible on the otolith and in all otoliths where a growth pattern could be identified, only in one fish was the number of annuli observed beyond the mark not equal to the number of years the fish had been at liberty after tagging. The OTC mark formed close to the edge of the otolith section (Fig. 5A), and the annual growth zones that formed beyond the mark were quite narrow (Fig. 5C), but did form annually. The average amount of otolith growth beyond the OTC mark for all fish examined was about one half of that shown in Fig. 5A.

The fish in the 1979 and 1980 samples ranged in age from 5 to 40 yr when tagged, and because each otolith added the number of annuli that corresponded to the years at liberty, it appears that the method is valid for all age-classes in the population. However, we would prefer to wait until more recoveries have been made over a period of up to at least 5 years before confirming that the method is valid for all age-groups within the population.

Most of these tagged and injected fish grew very little in length after release. Of the 39 fish sampled in 1980, 3 increased in length, 13 showed no change, and 22 decreased in length. The average change in length was −0.5 cm for females and −1.2 cm for males. Despite this poor growth in length, there was sufficient otolith growth in 33 of the 39 fish to identify an annual growth pattern. Thus the otolith is a sensitive recorder of annual growth patterns even during periods of poor growth.

Studies are currently underway to determine if the injections of OTC at the dosage used affects the amount of annual growth.

VALIDATION BY TAGGING STUDIES

A total of 36 fish that were tagged as part of the United States sablefish tagging program were made available by United States scientists to assist in the validation of the aging method. As these fish were at liberty for 6−8 years and many were quite small when marked, it was possible to estimate their age range when tagged using Fig. 6 and compare the sum of this age and the number of years at liberty with the age estimated from otoliths. Because young sablefish grow very rapidly, the error associated with estimating age from length for smaller sablefish was not believed to be large.

In most cases the ages determined using otoliths were similar to ages estimated from the tagging study (Table 1). In no case were fish aged much older than estimates from the tagging study. If errors occurred, they appeared to underestimate the true age.

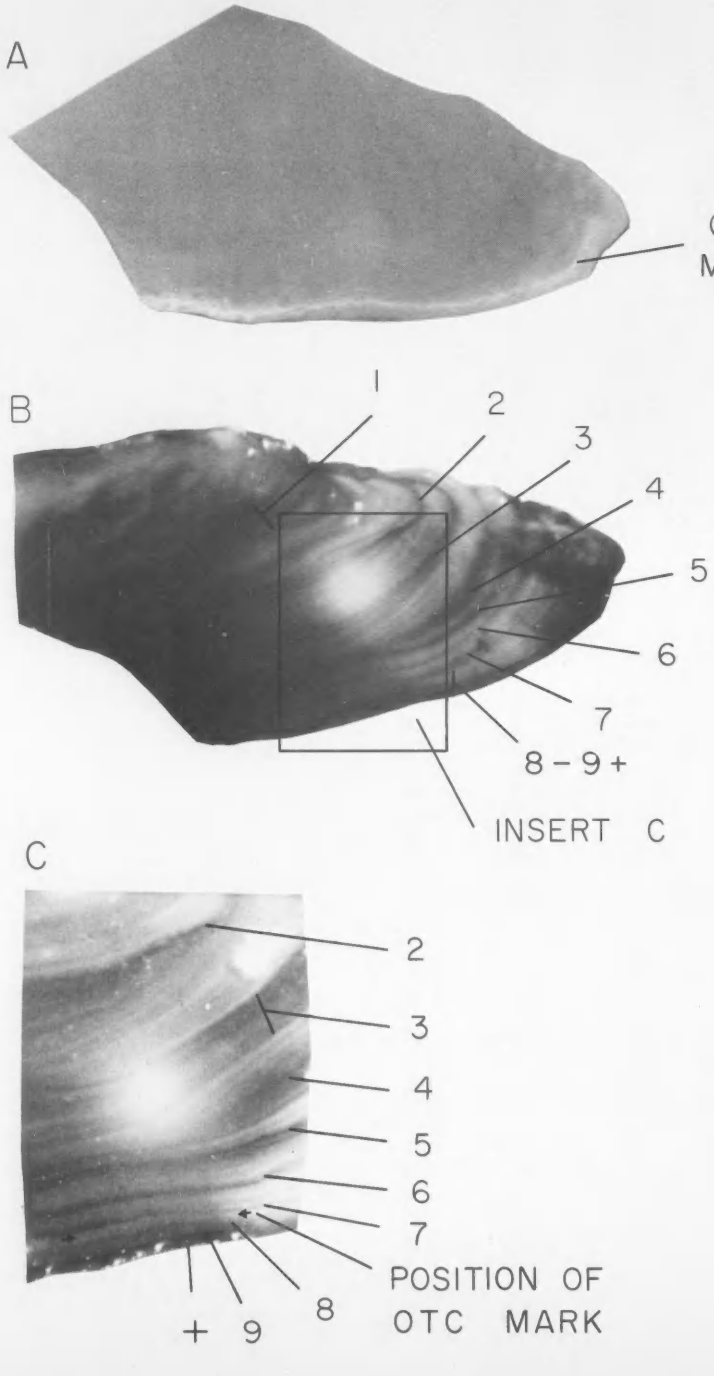
As most of the fish were quite small when tagged, there were few older fish in the sample. However, in one case a larger fish was tagged and recovered 7 yr later when it was aged as 22 yr. When recaptured, this female fish measured 75 cm and as this is an average size for female fish from the commercial fishery in the Canadian zone, it is additional evidence that the average age of female fish in the commercial fishery can range from 20 to 30 yr.

VALIDATION BY GROWTH ANALYSIS

Mean annual growth of mature untagged sablefish as estimated from ages determined from otoliths is small. The growth curves in Fig. 6 indicate that while there is variation in growth among areas, the annual growth increment ranges from 0.17 to 0.26 cm for males and 0.55 to 0.66 cm for females. There also was little mean positive growth for the 1911 tagged fish that were recovered between August 1977 and December 1979 (Table 2). If fish measured within several hours of recapture and prior to freezing or storing are treated separately from those that had been frozen or stored in ice or brine, a mean annual growth increment of 0.3 cm per year for all fish or 0.33 cm for fish recovered after 1 year or more was observed (Table 2). There was no significant difference in the growth increments of males and females.

Measurement errors at time of tagging and recapture do not appear to have been a contributing factor to the observed small growth increments. There was no difference in the mean lengths of the sample of 100 fish that received a second measurement prior to release after tagging or in a sample of 50 dead, tagged fish which were measured and remeasured.

FIG. 3. Sections of otoliths from known age sablefish. (A) A 68-cm male recaptured in May 1980 and aged 9+ yr. Arrows point to checks. The ninth annulus is difficult to identify. It is possible that the ninth annulus is a prominent check and the true annulus is on the edge. (B) A 77-cm female recaptured in April 1981 and aged 11 yr. It is possible that the third annulus is a check.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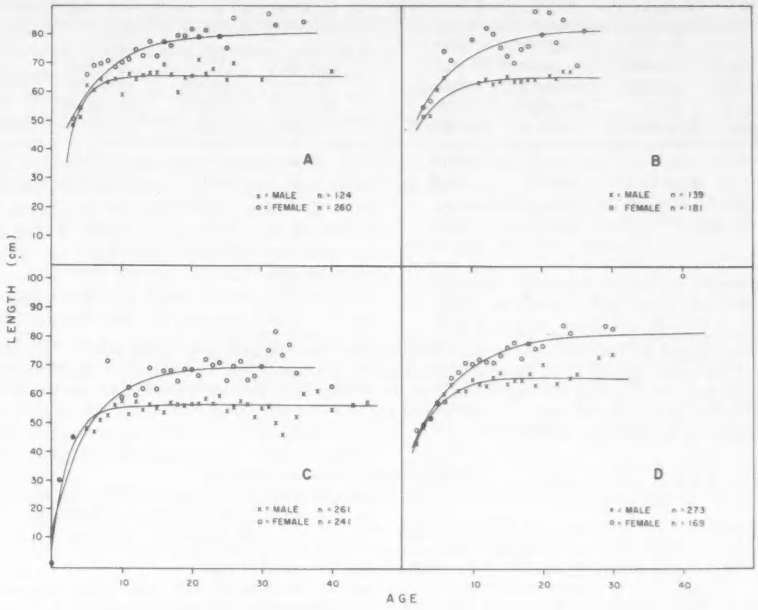

FIG. 6. Growth curves showing the variation in growth of some sablefish stocks sampled in 1979–80 off the west coast of British Columbia. Two samples from the west coast of Vancouver Island are included (C, D) to show the differences in size and age that can occur between samples collected in the same location. (A) West coast of the Queen Charlotte Islands: ♂: $K = 0.47$, $L\infty = 65.5$, $t_0 = 0.14$; ♀: $K = 0.16$, $L\infty = 80.8$, $t_0 = -3.51$. (B) Inlets east of Queen Charlotte Sound: ♂: $K = 0.26$, $L\infty = 64.6$, $t_0 = -2.91$; ♀: $K = 0.16$, $L\infty = 8.16$, $t_0 = -3.96$. (C) West coast of Vancouver Island: ♂: $K = 0.43$, $L\infty = 56.0$, $t_0 = -0.22$; ♀: $K = 0.19$, $L\infty = 69.5$, $t_0 = -0.99$. (D) West coast of Vancouver Island: ♂: $K = 0.29$, $L\infty = 65.7$, $t_0 = -1.75$; ♀: $K = 0.14$, $L\infty = 81.7$, $t_0 = -3.93$.

If measurement errors do occur, their frequency is probably equally distributed on either side of the true length, indicating that in large samples the net measurement error is negligible. There was a net average decrease of 0.5 cm when fish were measured after freezing and thawing indicating that freezing and handling contribute to the decrease (Table 2). Because a large number of recovered fish were examined and errors in measurements appear small, the slow growth indicated from the tagging study appears real and corroborates the slow rate of growth determined from the age estimates.

Sablefish in the Canadian fishery vary in average size depending on their sex and the capture location. Females grow to larger average sizes than males (Fig. 6) and in many areas less than 1% of the males are larger than 70 cm, compared with 58% for females (Beamish et al. 1978, 1979, 1980). The rate of annual growth of males was reduced before that of females (Fig. 6), and males and females continued to live for long periods during which little growth in length occurred.

While most of the larger fish are females, there are substantial numbers of fish of both sexes in the Canadian zone that are larger than the sizes of the recovered fish of known age (i.e. those tagged at age 1+ yr). Because of the reduced annual growth that was determined from the tagging studies, it is probable that these larger fish are considerably older than the known age 8- to 10-yr-old fish recovered from 1979 to 1981. Thus, ages ranging from 20 to 40 yr, as estimated from otolith readings (Fig. 6), do not appear unreasonable.

While the general assumption that large fish of either sex are older fish appears applicable, there are many individuals within some areas that are small and very old, making it difficult to apply any form of age-length key to the whole population.

FIG. 5. Cross section of otolith from a female sablefish that was tagged and injected with OTC in May 1978 at a length of 82 cm and recovered in August 1980 at a length of 84 cm. Fig. 5A shows the OTC mark that is yellow under UV light. Fig. 5B shows the section after burning. Burning destroys the OTC mark and unfortunately the annual growth zones were difficult to photograph so each annulus has been identified. Fig. 5C is an enlargement of the growth zones that formed before and after the OTC mark. Again, the annuli have been identified. The arrows in Fig. 5C indicate the position of the OTC mark. It is possible to identify the remaining growth and annulus for 1978, the 1979 growth and annulus, and 1980 growth.

TABLE 1. Comparison of ages determined from otoliths and estimated from the United States tagging study.[a]

Tagging length male and female (cm)	Estimated[b] age from length at tagging	Yr of growth prior to recapture, ♂	Age at recapture estimated from tagging study, ♂	Age estimated from otoliths, ♂	*n*, ♂	Estimated age from length at tagging	Yr of growth prior to recapture, ♀	Age at recapture estimated from tagging studies, ♀	Age estimated from otoliths, ♀	*n*, ♀
50–55	4–6	8	12–14	12.0	2	4–6	8	12–14	12.7	3
		6	10–12	12.0	1		7	11–13	13.5	3
56–60	5–8	8	13–16	11.5	2	5–7	8	13–15	13.5	2
		7	12–15	13.0	4		7	12–14	12.4	5
							6	11–13	12.0	1
61–65	7	8	15	13.0	1	6–10				
		7	14	16.0	2		7	13–17	14.5	2
		6	13	13.0	1		6	12–16	14.7	3

[a]One 35-cm fish when tagged was not sexed when recaptured 8 years later. The estimated age at tagging was 2–3 yr and age at recapture would be 10–11 yr. The otolith age was 12 yr. Three fish measuring 46–55 cm also were not sexed when recaptured 7 years later. The estimated age at tagging was 4–6 yr and age at recapture 11–13 yr. The average age from otoliths was 13.8 yr. One 67-cm fish when tagged was recovered 7 years later, sex was female and otolith age was 22 yr.

[b]Estimate was made using the data used for Fig. 6.

TABLE 2. Average growth of recovered sablefish.

	All recovered sablefish			Only sablefish measured by fisheries staff within 1 h of recapture		
Years after tagging[a]	Avg. growth (cm)	SD	*n*	Avg. growth (cm)	SD	*n*
0	−0.6	1.3	187	−0.1	0.9	15
0.5	−0.5	1.1	734	−0.2	0.9	112
1	−0.5	1.4	589	+0.3	1.6	77
1.5	−0.6	1.5	334	+0.2	1.5	16
2	−0.3	1.4	51	+0.7	1.6	9
2.5	−0.7	1.1	16	+0.0	1.4	2

[a]One growing season is arbitrarily assumed to be from May 1 to September 30. A tagged fish has completed 0.5 of a growing season after any 2.5-mo period between May 1 and September 30.

Discussion

The most reliable method fishery biologists have for estimating the age of fishes requires that a pattern of growth be identified on some structure from the fish. The pattern must then be related to the annual growth history of the structure and if separately identifiable growth zones within the pattern form only once a year, one zone can be considered an annulus. However, it is essential that the pattern be shown to form throughout the life of the individual. For example, it is known that the pattern of circuli growth observed on scales of some fish can change abruptly (Beamish 1973). Because scales grow to protect fish, it is not unreasonable that scale growth should become retarded once growth of fish is reduced. It is also known that as otoliths grow, the area of growth may be restricted to the internal surface (Irie 1960; Mugiya 1974). Such a change in otolith growth would alter the growth pattern if viewed from the external surface. Thus, an examination of a cross section of an otolith may be the most appropriate method of aging older fish. It is a mistake to choose a structure simply because it has been useful for some other species or stock. We rejected the use of scales because we could not consistently recognize any pattern of circuli formation. A weak pattern was observed on some sections of fin rays, but only a few growth zones could be counted. There were zones that appeared on the external surface of the otolith, but it was rarely possible to identify a pattern of zone formation. Only on the transverse section of the otolith was there an obvious pattern of growth zone development. Because the pattern appears to form throughout the life of the fish, the age of sablefish was estimated from broken sections of otoliths. Burning and treating with cedar wood oil enhanced the contrast between growth zones.

The method developed for estimating the age of sablefish indicates that sablefish are much older than formerly thought. While the interpretation of the growth pattern on otolith sections may be questioned because it has not been validated for a large number of samples, it was valid for the examples tested. Known aged fish that were tagged, released, and recovered 8 and 9 years later had added about eight or nine annual growth zones to the otolith. While there was an error involved in the interpretation of annual growth zones, there was no indication that the zone identified as an annulus formed more than once a year. The application of an oxytetracycline mark in the otolith of tagged fish confirmed that the zone identified as an annulus formed once a year for fish of a range of ages. The analysis of age of recaptured sablefish that were tagged at a small size and were at liberty for 6–8

years indicated that ages determined by the breaking and burning technique were within the expected age range. In particular, there was no indication that fish were significantly overaged as a consequence of considering that more than one translucent zone formed in 1 year. And finally, evidence of a low rate of growth beyond the first few years as determined by the otolith ages was corroborated by the results of tagging. In contrast, the ages determined from scales (Pruter 1954 and others) indicated that the rate of growth was much faster and that most sablefish in the commercial size range were 5–10 yr rather than 8–45 yr as indicated from the otolith sections. However, the scale method has not been validated for adult fish and it has been demonstrated to be unreliable for other slow-growing, long-lived fishes (Aass 1972; Beamish 1973; Mills and Beamish 1980). We can accept that there are some difficulties with our method of age determination, but there is no reason to reject the ages determined using the growth pattern on the broken and burnt section of the otolith simply because they do not agree with ages estimated from scales or because we have some anthropomorphic difficulties accepting that some fishes have longevities approaching that of man.

The slow growth rate suggests that there is a large number of age-groups in the commercial catch and the instantaneous natural mortality rates are much lower than formerly thought (Low et al. 1976). A management strategy that assumes fast growth and few age-groups and encourages heavy fishing clearly could result in overfishing and a drastic reduction in the number of age-groups available to the fishery. If the need for either a large number of age-groups in sablefish populations or a number of very old fish or both is in response to long periods of poor environmental conditions, then an error in management strategies, coupled with a number of consecutive years of poor environmental conditions, could result in a major recruitment failure and a collapse of a commercial fishery.

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Growth and Maturation of Southwest Nova Scotia Atlantic Herring (*Clupea harengus harengus*)

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SINCLAIR, M., A. SINCLAIR, AND T. D. ILES. 1982. Growth and maturation of southwest Nova Scotia Atlantic herring (*Clupea harengus harengus*). Can. J. Fish. Aquat. Sci. 39: 288–295.

Juvenile and adult growth rates, and the maturation schedule, for the southwest Nova Scotia herring stock (NAFO SA 4WX) were investigated over the period 1968–78. The variance in juvenile (age 2) summer growth is not well accounted for by initial weight, juvenile population abundance, and temperature unless a discontinuity in growth pattern starting in 1970 is accounted for. Length at maturity and at recruitment to the adult schools appears to be inversely related to the population abundance experienced during juvenile growth. However, at very low juvenile population size, maturation appears to be inhibited. Somatic growth rate and its year-to-year variability decreases close to an order of magnitude with the onset of maturation. Because of this decrease with age and the radical shifts in age composition with time, population growth rate fluctuates markedly. Because high population abundance parallels downward shifts in age composition, there is a clear, positive relationship between population growth rate and population abundance. There is a dome-shaped relationship between cohort somatic growth rate and cohort size at intermediate ages, suggesting that over a broad range in population size, adult growth rate is not density-dependent. This growth response is interpreted in relation to planktivorous feeding in a patchy environment. Strong year-class strength variability coupled with a marked decline in somatic growth rate with age results in non-steady state population production. When the age composition is biased towards older ages, catch (defined by $F_{0.1}$ guidelines) exceeds population production resulting in rapid stock declines. The growth characteristics of herring are discussed in relation to the literature and "analytical" yield models.

Key words: Atlantic herring, growth, maturation, production

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De 1968 à 1978, nous avons étudié les taux de croissance de harengs juvéniles et adultes, ainsi que le calendrier de maturation chez le stock du sud-ouest de la Nouvelle-Écosse (divisions 4WX de l'OPANO). Les poids initiaux, l'abondance de la population de juvéniles et la température n'expliquent pas la variance observée de la croissance estivale des jeunes (âge 2), à moins qu'on ne puisse expliquer une discontinuité dans l'évolution de la croissance à partir de 1970. La longueur à la maturité et au recrutement des bancs adultes semble inversement reliée à l'importance de la population pendant la phase de croissance juvénile. Cependant, avec des effectifs de population de juvéniles très bas, la maturation semble entravée. Le taux de croissance somatique et sa variabilité d'année en année diminuent de près d'un ordre de grandeur avec le début de la maturation. Par suite de cette diminution en fonction de l'âge et des glissements radicaux de la composition par âge avec le temps, le taux de croissance de la population fluctue de façon marquée. Étant donné que des effectifs de population importants sont accompagnés de glissements vers le bas de la composition par âge, il existe une relation positive évidente entre le taux de croissance de la population et l'abondance de cette dernière. Il y a relation en forme de dôme entre le taux de croissance somatique des cohortes et la taille des cohortes à des âges intermédiaires, ce qui laisse supposer que le taux de croissance n'est pas dépendant de la densité sur une gamme étendue d'effectifs de population adulte. Nous interprétons cette croissance comme étant une réponse liée à une alimentation planctivore dans un environnement caractérisé par des taches planc-

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tonique. Une production de population non en équilibre est le résultat d'une forte variabilité de l'abondance des classes d'âge couplée à un déclin marqué du taux de croissance somatique. Quand la composition par âge est biaisée vers des âges plus avancés, les prises (définies d'après les lignes directrices de $F_{0.1}$) dépassent la production de la population et il en résulte des déclins rapides du stock. Nous analysons les caractéristiques du hareng en relation avec les travaux publiés et les modèles de rendement « analytiques ».

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AN understanding of the factors controlling growth rates and the age at maturity in exploited fish populations is of both fundamental and applied interest. The manner by which natural populations respond to fluctuations in their abundance and to environmental factors, although well studied, is still a central issue in population biology. Exploited populations are frequently subjected to more dramatic fluctuations in abundance, so population responses may be more evident than those observed in populations less perturbed by human activities.

The two classes of yield models used in fisheries management make assumptions concerning the manner in which populations grow at different age compositions and overall stock levels. In the surplus production models (Graham 1935; Schaefer 1954) it is assumed that rates of growth, survival, or recruitment tend to decrease as biomass increases and vice versa. The analytical models or yield per recruit models (Baranov 1918; Beverton and Holt 1957) assume steady state conditions and often, at least in their application, that growth rates are relatively constant with changes in biomass.

Within the above framework (population biology and/or fisheries management), "density dependent" changes in growth rates at various life history phases and changes in age or length at maturity have been documented for several stocks (Ware (1980) discusses much of the literature). However, for pelagic stocks the evidence for density-dependent growth and maturation is contradictory. In this study the juvenile and adult growth rates and the maturation schedule are investigated for the southwest Nova Scotia herring stock (NAFO SA 4WX). Subsequently some implications of the growth characteristics of herring on stock assessment methodology are addressed.

Methods

The Canadian herring catch from the NAFO subarea 4WX management unit has been sampled in considerable detail for length frequencies and biological parameters since 1968. Before 1968, less detailed sampling of the catch was carried out. It is from this accumulated data base on characteristics of the catch that growth and maturity characteristics of the population are inferred. This assumes that the fishery adequately samples the population, and the port samples the catch.

Mean lengths and weights at age for a given month and gear type were estimated using both the length frequency samples and the detailed biological samples. Removals at age by 1-cm-length intervals were calculated from the sample length frequencies, the derived age-length keys, and length–weight relationships. These data are routinely generated each year in preparing stock assessments.

Mean length at 50% maturity was calculated by sex from the detailed biological samples. A maturity stage-length key was constructed using only the August samples from the purse-seine fleet. Fish at or above stage 3 (following Parrish and Saville 1965) were considered mature. There may be some bias towards overestimating the percent maturity at length by using the samples close to the spawning period (August), but the between-year comparisons should be valid. The mean length at 50% maturity was calculated from a linear regression of percent mature against length. The relationships were more satisfactorily described using linear regressions than probit regressions.

Population and cohort annual production were estimated from the yearly (July to July) increase in weight. Cohort production is as follows:

$$P_i = (w_i - w_{i-1}) \cdot N_i$$

where P_i = production by cohort at age i, w_i = July weight at age i herring, w_{i-1} = July weight of age $i-1$ herring, and N_i = January 1st cohort abundance of age i herring.

Population annual production (P) (i.e. for ages $2\frac{1}{2}$ and older) is

$$P = \sum_{i=3}^{10} P_i = \sum_{i=3}^{10} (w_i - w_{i-1}) \cdot N_i.$$

The average biomass of a cohort (b_i) within the July to July period was estimated by the equation:

$$b_i = \frac{w_i + w_{i-1}}{2} \cdot N_i$$

and the average population biomass (B) by:

$$B = \sum_{i=3}^{10} b_i = \sum_{i=3}^{10} \frac{w_i + w_{i-1}}{2} \cdot N_i.$$

Annual growth rate of a cohort $[g_i = w^{-1}(dw/dt)]$ was estimated by $\Delta w/w$ or

$$g_i = \frac{2(w_i - w_{i-1})}{w_i + w_{i-1}}.$$

This estimate of growth rate approximates instantaneous growth rate (Ricker 1975). The corresponding population growth rate (G) was estimated by P/B.

Note that only somatic growth is considered in the above definitions. As there is no time series data on gonad weights for this stock (4WX herring), production of sexual products cannot be considered.

Results

JUVENILE SUMMER GROWTH

Sinclair et al. (1981) observed that there was a marked

TABLE 1. Correlation coefficients and multiple regression coefficients from the growth analysis. (Basic data available from authors on request.)

	Initial weight (ln w)	Abundance estimate 1 (N_1)	Abundance estimate 2 (N_2)	Temp. (T)
		Correlations		
Weight increment	0.09	−0.39	−0.49	0.20
Variable	Coefficient	SE	T-value	Variation
		Multiple regression		
		Dependent variable — ln Δw		
		Independent variable — ln w, N, T		
ln w	0.272	0.404	0.67	2.6
N_2	−0.100	0.056	−1.77	23.5
T	−0.00843	0.253	0.33	0.8
		Multiple regression		
		Dependent variable — ln Δw		
		Independent variable — ln w, N, T, dummy		
ln w	−0.400	0.305	−1.31	13.11
N	−0.060	0.037	−1.62	3.66
T	−0.023	0.016	−0.42	5.89
Dummy	0.579	0.144	−4.02	51.22
Intercept = 5.17				
R^2 (%) = 73.9				

change in the early 1970s in the relationship between summer increase in length (May−September) and initial length. In addition, there was some indication that summer length increment, when corrected for the length-dependent bias (Iles 1967), was inversely related to juvenile population abundance, but unrelated to summer temperature. It is of interest and consistent with the following treatment of adult growth to consider the summer growth of 2-yr-olds in weight rather than length. The following equation was used:

$$(1) \qquad \Delta W = aW^b e^{cN} e^{dT}$$

where ΔW = summer growth increment (in grams) (from May to September); W = initial body weight in May (in grams); N = 'competing' population density; T = summer temperature (°C) (sum of the monthly means from May through September); and a, b, c, and d are fitted coefficients.

Equation (1) assumes that the growth increment for a particular year-class is a multiplicative function of initial body size, water temperature, and year-class abundance. Because the 2-yr-old juveniles coexist with a large part of the preceding 3-yr-old cohort (approximately one-third of the 3-yr-olds recruit to the adult population), and the frequency of good year-classes has decreased with time (Sinclair et al. 1979), it was thought appropriate to consider the potentially competing population density (N_2, abundance of 2-yr-olds plus two-thirds of 3-yr-olds) as well as the abundance of the year-class at age 2 (N_1). N_1 and N_2 were estimating using cohort analysis (Pope 1972). The N_1 values are very similar to those shown in Sinclair and Iles (1980), where the methodology is explained in detail. The ΔW and W values were estimated from the length data using the following length−weight relationships:

$$W = 0.0042\ L^{3.23} \text{ (May)}$$
$$W = 0.00290\ L^{3.30} \text{ (September)}.$$

The constants for the length−weight relationships are the means of the values estimated from the detailed biological samples from the New Brunswick weir fishery in 1977 and 1978. It is assumed that the length−weight relationship observed during 1977 and 1978 is representative of the earlier years treated in the analysis.

The transformation for estimating the constants in equation (1) by linear regression is

$$\ln(\Delta W) = \ln a + b(\ln W) + cN + dT.$$

Although not significant at the 5% level, N_2 is better correlated (negatively) with summer growth than is N_1 (year-class size) (Table 1). Temperature is not strongly correlated with summer growth, but the sign is in the expected direction. The multiple regression, in which N_2 is the population density variable, has an R^2 of only 0.269. The results of the analysis indicate that (when all years are considered) initial weight, population density, and temperature do not explain a large part of the variance in juvenile (age 2) summer growth. No doubt the change in the growth pattern that was observed in Sinclair et al. (1981), which may be due to a change in the population composition in the juvenile weir fishery, complicates the analysis.

When a dummy variable is added to the regression analysis to account for the suggested discontinuous growth pattern in time (due to proposed stock compositional change beginning in 1970), there is a considerable increase in the R^2 value from 26.9 to 73.9 (Table 1). In this analysis, the regression equation takes the form:

$$\ln(\Delta W) = \ln a + b(\ln W) + cN + dT + eD$$

where D is the dummy variable (D = 0 for 1965−70; D = 1 for 1971−78).

The results, although thought to be confounded by stock

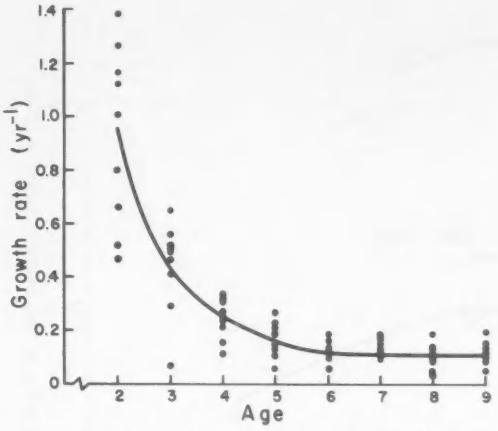

FIG. 1. Somatic growth rate as a function of age for the NAFO subarea 4WX herring stock.

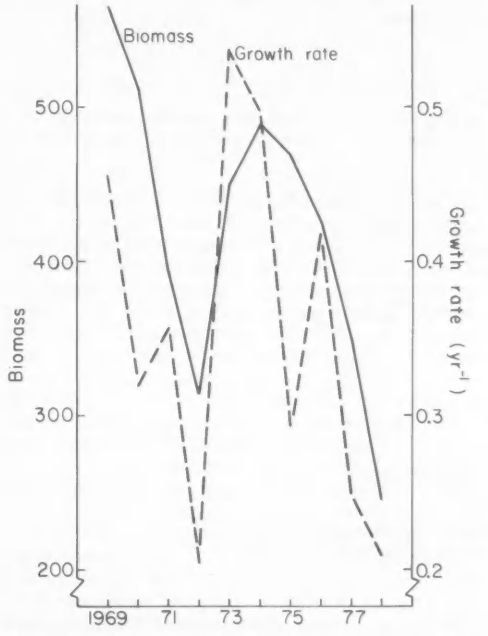

FIG. 2. Temporal distribution of growth rate and biomass (in thousand tons) for the NAFO subarea 4WX herring stock.

compositional changes in the juvenile fishery, are not inconsistent with density-dependent juvenile growth.

ANNUAL GROWTH RATES AT AGE

The mean July lengths and weights for ages 2–10 from Nova Scotia weirs and purse seines were weighted by removals at age to provide overall means. The estimates of population biomass, production, and growth rate (P/B) are available from the authors upon request.

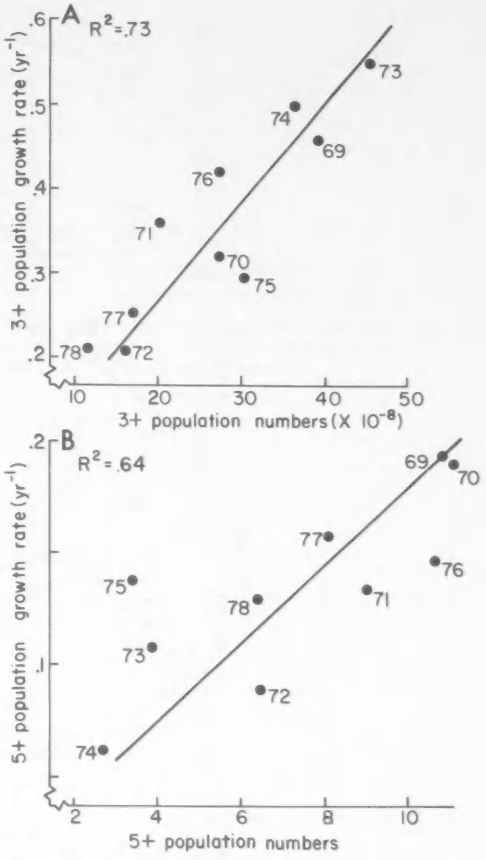

FIG. 3. The relationship between population growth rate and population abundance (in hundred millions) for the NAFO subarea 4WX herring stock. In the upper graph ages $2\frac{1}{2}$ and older are considered while in the lower graph only ages 5 and older are considered.

The somatic growth rate declines rapidly with age, close to an order of magnitude between ages 2 and 6 (Fig. 1). Also, the year-to-year variability in growth rate, in absolute terms, declines in a parallel fashion. Figure 2 shows a parallel distribution of population growth rate (P/B) and population biomass. This demonstrates that for non-steady state populations such as herring, population growth rate is highly variable and associated with population biomass. The greater the stock size, the higher the growth rate. In part, this is clearly an age composition effect. The population biomass is at its largest when strong year-classes are recruiting to the fishery. At such time, the population is dominated by younger fish with higher growth rates (Fig. 1). Because of this strong age composition effect on population growth rate, it is not surprising that there is a significant relationship with population abundance (Fig.

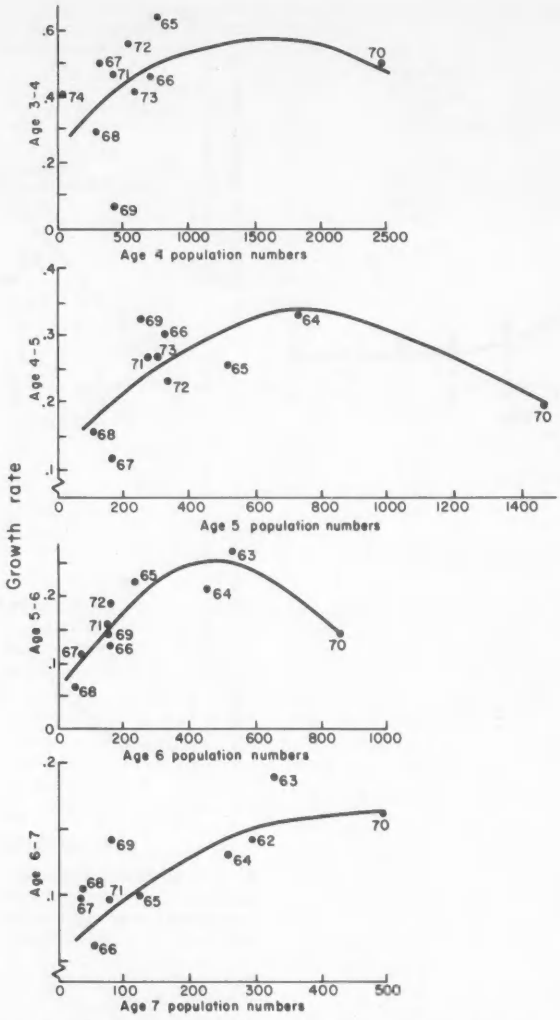

FIG. 4. Cohort growth rate in relation to cohort abundance (in millions) for the NAFO subarea 4WX stock. Year-classes are indicated.

3A). The points for 1976–77 and 1977–78 were not included in the calculation of R^2 because of the higher probability of error in the estimation of population numbers obtained from the most recent years in the cohort analysis.

However, a plot of recruited population growth rate (5+) versus recruited population numbers (5+), which minimizes the age composition effect, also indicates a positive relationship (Fig. 3B). To investigate further the importance of population abundance on growth rate, individual cohorts were considered (Fig. 4). The analysis suggests that for intermediate ages, there is a dome-shaped relationship between growth rate and cohort size. The exceptionally large 1970 year-class has a relatively depressed growth rate at intermediate ages. As this cohort decreases in abundance, by age 6 to 7, the relationship appears more asymptotic. Thus, overall, there is an unexpected positive relationship between somatic growth and population abundance.

MATURATION

There is evidence for a positive relationship between length at recruitment to the purse-seine fishery and length at 50% maturity (Fig. 5). The relationship between length at recruitment (as estimated by mean length of age 3 fish caught

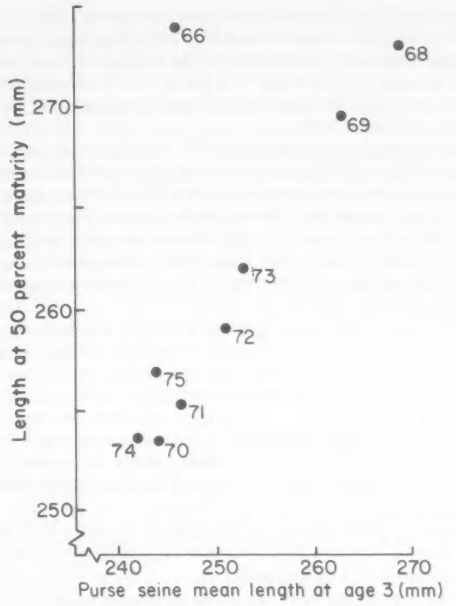

FIG. 5. Relationship between mean length at 50% maturity and mean length at age 3 in the purse-seine fishery. Year-classes are indicated.

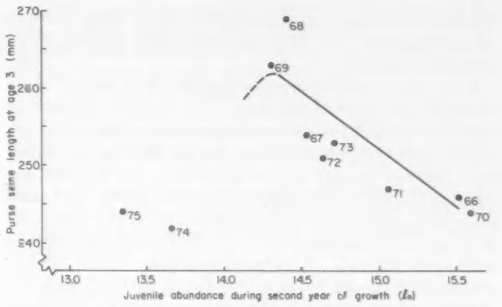

FIG. 6. Relationship between age 3 mean length in the purse-seine fishery and juvenile abundance in the previous year. In (age 2 + $\frac{2}{3}$ age 3) $\times 10^{-3}$. Year-classes are indicated.

in the summer purse-seine fishery) and population size during juvenile growth (abundance of juveniles, age 2 plus $\frac{2}{3}$ of age 3 cohorts, during the previous year) is complex (Fig. 6). Over a broad range in population size, there is a decrease in length at recruitment with increasing cohort size suggesting density dependence. If there is a corresponding decrease in mean length at age 3 with increasing cohort size over the same population range, then the age at 50% maturity would be relatively constant.

The two most recent year-classes, 1974 and 1975, for which the maturing year-classes were exceptionally small, recruited and matured at a relatively small length. Because the mean length at age 3 was also small for these years (Fig. 6), the age at maturation may not have shifted downwards. The decrease in length at recruitment, and length at 50% maturity, for the extremely small year-classes is an unexpected result. It suggests that below some critical population level, density-dependent processes may not function.

BIOMASS, PRODUCTION, AND CATCH

Production and catch as presented in Fig. 7 were calculated from July to July. The catch is that taken in the 4WXa fishery plus 30% of the New Brunswick weir catch (to be consistent with the cohort analysis numbers at age estimates, which are used in calculation of production). The catch includes age 2+ fish from August to December and age 3+ from January to July. Two estimates of population biomass are indicated, that on January 1st and the remaining biomass of the same year-classes on December 31st. Thus, for the production and catch

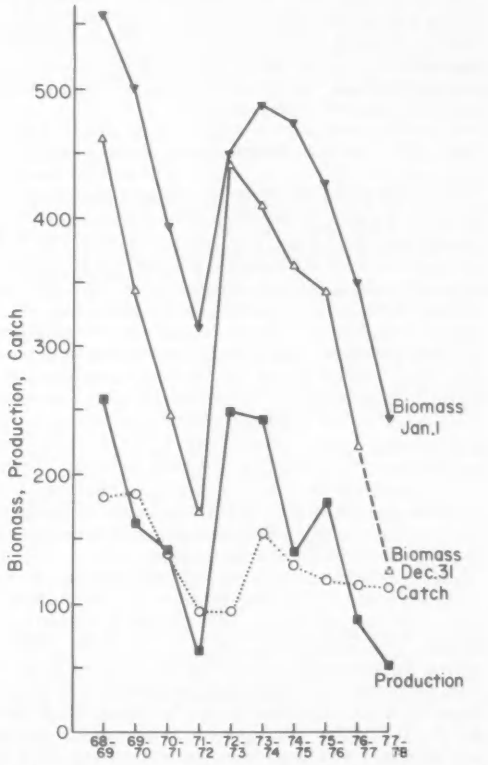

FIG. 7. Temporal trends in biomass (in thousand tons) production and catch for the NAFO subarea 4WX herring stock.

year 1968-69, the biomass estimates are for January 1, 1969 and December 31, 1969. The difference between the January and December biomass estimates is due to the decrease in biomass from mortality (both fishing and natural) less the increase in biomass from production. The increase in biomass shown between December 31st of 1 year and January 1st of

the next is the result of recruitment at age 3. Thus, it can be seen that at age 3, the 1970 year-class added 280 000 t to the population biomass.

Catch has exceeded production during two periods, from 1969–70 to 1971–72 and from 1977–78 to the present. In the former period, stock biomass was reduced sharply through a period of average recruitment. During this time the difference between January 1st and December 31st biomass was close to 150 000 t. The appearance of the strong 1970 year-class increased biomass and production, but not as high as the 1970 level. During this interval, production was greater than catch until 1976–77. Very poor recruitment in the two following years caused production to fall to 50 000 t, while the catch remained at 100 000 t. Biomass on January 1, 1978 was estimated to be 224 000 t and given that the 1978 catch was twice that of the estimated production, the December 31, 1978 biomass was likely to be in the region of 125 000 t, a critically and historically low level. However, current indications are that the 1976 year-class is large and thus stock biomass will be on another upward swing. The observation of interest here is that during two periods when the age composition was biased towards older ages, the catch exceeded somatic production of the population.

Discussion

There are contradictions in the literature concerning the existence of density-dependent growth and maturation in both juvenile and adult herring. Iles (1967), Anthony (1971), Lett and Kohler (1976), and Hubold (1978) have shown evidence for density dependence in juvenile growth. Moores and Winters (1978) did not observe density-dependent age 1 (L_1) length for Gulf of St. Lawrence herring using the same data as Lett and Kohler (1976) and suggested that the latter study used faulty criteria in the interpretation of the raw data. Again, Lett and Kohler (1976) and Winters (1976) arrived at opposite conclusions concerning density-dependent growth of adult herring in the southern Gulf of St. Lawrence. Lett and Kohler (1976) found no evidence, whereas Winters (1976) concluded that there is density dependence. Lett (1978) argued that Winters' (1976) conclusions are invalid as they are based on mean lengths and weights at age in relation to population biomass, and not on growth rate. Iles (1971) showed some evidence for adult density-dependent growth for North Sea herring. Unfortunately other studies on North Sea adult herring growth (Wood 1965; Cushing and Burd 1957; Hubold 1978; Burd 1978; Saville 1978) do not directly address the problem of growth rate at age in relation to cohort size. Grosslein et al. (1980) concluded that there is no evidence for density-dependent growth by Georges Bank adult herring. If anything, there appeared to be increased growth rate associated with larger year-classes (Dornheim 1975, as cited by Grosslein et al. 1980).

There is less information concerning shifts in maturation at length or at age for Atlantic herring (*Clupea harengus harengus*). Winters (1976) indicated a downwards shift in the age at 50% maturity for both spring and autumn spawners as the adult population biomass decreased (3.8–3.5 for spring and 5.9–5.2 for autumn). Hubold (1978) showed some evidence for similar shifts in maturity at age for North Sea herring. Parrish and Saville (1965) reported the decrease in age of maturity for North Sea herring in the early 1950s. Lett (1978) found no evidence for shift in either length at maturity or age at maturity for mackerel in the Gulf of St. Lawrence and actually suggested that "the ability to shift their maturity ogive in relation to length is a basic difference between pelagic and demersal fish."

In summary, there appears to be some coherence in the observations on juvenile density-dependent growth (with the exception of Moores and Winters 1978), but there are contradictions in the literature on adult growth. This may be partly due to the looseness of growth terminology. Changes in length or weight at age are frequently, and incorrectly, used in arguments concerning growth in relation to population density.

The analysis of juvenile growth in relation to cohort size is confounded by temporal changes in the stock composition in the area of maximal Canadian juvenile catches. Nevertheless the results of this study tend to confirm the conclusions concerning juvenile growth, but differ in the other two aspects (adult growth and maturation). Length at recruitment to the adult population and length at 50% maturity fluctuate in a density-dependent fashion in response to the juvenile population size that was experienced. This may result, however, in a relatively fixed maturity at age schedule in contrast to conclusions of Winters (1976) and Hubold (1978), but in partial agreement with Lett's hypothesis.

The unexpected result was the evidence for a positive relationship between somatic growth rate of adults and cohort density, as was found by Dornheim (1975) for Georges Bank herring. For a schooling fish in a patchy environment, this might be interpreted in energetic terms. If the overall abundance of food for adult herring is non-limiting, but distributed in patches, and herring school size increases with cohort abundance, then it is possible that at increasing population density, the overall food abundance is more efficiently located, i.e. more patches of food per day are found when the schools are larger, (MacKay 1976; Olson 1964; Radokov 1972; Eggers 1976). This interpretation of the observations assumes that there are behavioral mechanisms involved in schooling, so that the information concerning the location of a food patch is passed between individuals and that the patch sizes are large enough, so that the increased location of patches per day, for example, is not negated by the decrease in individual food consumption per day as a result of the increase in fish per school. Clearly, the interpretation is speculative, but it is attractive in that it suggests an energetic basis for the evolutionary advantage of schooling.

An alternative interpretation is that the acquisition of surplus energy is density-dependent, but growth rate itself is not (Ware 1980). If surplus energy was allocated to reproduction in a density-dependent fashion, which in adult herring accounts for about 90% of the surplus energy, it is possible that growth rate is affected in the manner described in Fig. 4.

The rapid decline in somatic growth rate of herring with age causes population production to decrease sharply when several recruiting year-classes in a row are weak. This characteristic of herring populations may have serious implications for the use of the "analytical" models for this species. These models assume steady state conditions with resultant stable age composition. Following this assumption, annual population production is equal to the sum of the annual productions

of a single cohort over its entire life. Annual MSY can then be estimated by analyzing the maximum yield that can be taken from a single cohort's production as it passes through the fishery.

When the stable age composition assumption is seriously in error (biased towards older ages), coupled with rapid decrease in somatic growth rate in the case of herring, the annual production of the population is no longer equal to the production of a single cohort throughout its life. In fact it is much lower, thus the F_{MSY} and even the more conservative $F_{0.1}$ (Gulland 1968) generated TACs may be inappropriate. It is possible that the relationship between somatic production and catch for herring may be a useful criterion for management purposes. For example, when the $F_{0.1}$ catch exceeds production, this guideline could be replaced by a "surplus production" guideline.

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Overestimation of Orthophosphorus Concentrations in Surface Waters of Southern Lake Michigan: Effects of Acid and Ammonium Molybdate[1]

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Water from southern Lake Michigan was analyzed to determine if orthophosphorus (PO_4-P) concentrations are overestimated by molybdenum blue methods and to assess the potential effects of ammonium molybdate on soluble reactive phosphorus (SRP) determinations. Time-course "hydrolysis" tests, based on the Chamberlain–Shapiro extraction method, showed that large amounts of PO_4-P were released from bound sources into solution within seconds after acid molybdate was added, and that molybdate-reactive PO_4-P could be retained by filters or released from particulate material into filtrates during filtration. PO_4-P concentrations obtained by using the prescribed exposure of 30 s were overestimated minimally by up to 86%, and ammonium molybdate dramatically accelerated PO_4-P release in filtered samples. Tests using up to a fourfold range in ammonium molybdate concentrations also showed that the extraction method and Harvey's method yielded SRP values that varied two- to three-fold or more, and that most of the PO_4-P was released from "particles" in filtrates. Analytical methods, therefore, can yield substantially different SRP estimates because of differences in the length of time samples are exposed to acid molybdate and because of differences in molybdate concentrations.

Key words: ammonium molybdate, hydrolysis, phosphorus, soluble reactive phosphorus, orthophosphorus

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Des analyses ont été effectuées sur l'eau du sud du lac Michigan en vue de déterminer si les méthodes au bleu de molybdène surestiment les concentrations d'orthophosphore (PO_4-P) et d'évaluer les effets possibles du molybdate d'ammonium sur les dosages de phosphore réactif soluble (SRP). Des essais d'« hydrolyse », fondés sur la méthode d'extraction de Chamberlain–Shapiro, indiquent que de fortes quantités de PO_4-P sont libérées dans la solution quelques secondes seulement après addition du molybdate acide et que le PO_4-P réagissant au molybdate pouvait être retenu par des filtres ou mis en liberté à partir du matériel particulaire dans les filtrats au cours de la filtration. Les concentrations de PO_4-P obtenues à la suite de l'exposition conseillée de 30 s sont surestimées minimalement jusqu'à 86%, et le molybdate d'ammonium accélère de façon dramatique la mise en liberté du PO_4-P dans les échantillons filtrés. Des essais dans lesquels on utilise des concentrations de molybdate d'ammonium dans une gamme quatre fois plus étendue indiquent également que la méthode d'extraction et la méthode de Harvey donnent des valeurs de SRP variant du double ou du triple et plus, et que la plus grande partie du PO_4-P est mise en liberté à partir de « particules » dans les filtrats. Les méthodes analytiques peuvent donc donner des estimations de SRP substantiellement différentes par suite de différences de durée d'exposition des échantillons au molybdate acide et de différences de concentrations de molybdate.

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MOLYBDENUM blue methods are believed to overestimate orthophosphorus (PO_4-P) concentrations in filtered lake water because PO_4-P is released from bound sources by hydrolysis (cf., Rigler 1973; Olsen 1967). Analytical PO_4-P measurements, therefore, are termed soluble reactive phosphorus (SRP) to distinguish them from PO_4-P concentrations in samples before acid reagents are added (Strickland and Parsons 1965). Evidence that overestimation occurs is based on several types of tests: SRP concentrations can be reduced 50–80% by centrifuging or refiltering 0.45-μm filtrates through 0.1-μm filters (Chamberlain 1968; Rigler 1973), anion-exchange resins are unable to remove 25–70% of molybdate-reactive PO_4-P from filtrates (Jones and Spencer 1963; Rigler 1968), and PO_4-P can be released from colloids when filtrates are treated with molybdenum blue reagents (Paerl and Downes 1978; Stainton 1980). Moreover, PO_4-P may be overestimated if algae leak PO_4-P or acid-labile compounds into filtrates during filtration (King 1970; Rigler 1973).

A tacit assumption in molybdenum blue methodology is that the amount of PO_4-P released by hydrolysis increases with acid exposure time and that hydrolysis rates increase with higher acid levels. This belief has motivated development of methods using weaker acid or shorter acid contact times (Chamberlain and Shapiro 1973; Olsen 1967). Weil-Malherbe and Green (1951) and Lutwack and Sacks (1952), however, showed that ammonium molybdate catalyzes acid hydrolysis rates of organic and condensed inorganic compounds and that the effects are concentration dependent. Because the pool of dissolved organic matter in lake water is composed of relatively weak P—O—C bonds (Golterman 1973), molybdate may accelerate PO_4-P release rates from organic or other bound sources in filtered lake water.

Previous tests showing that molybdenum blue methods overestimate PO_4-P concentrations leave three important questions unanswered. First, what is the magnitude of the discrepancy between SRP and true PO_4-P concentrations? Rigler (1966), for example, demonstrated that analytical methods overestimated maximum possible PO_4-P concentrations in several lakes in Ontario, Canada, by factors of 10 to 100, but Chamberlain and Shapiro (1969) could not detect "hydrolysis" in water from Minnesota lakes and showed that SRP estimates, after correction for arsenate interference, were equivalent to biologically available P (i.e. presumably PO_4-P). Second, what is the rate at which PO_4-P is released from bound sources in filtrates and does molybdate affect acid release rates? Few attempts to measure "hydrolysis" rates have been made, the results are conflicting, and the potential effects of molybdate have been ignored. Paerl and Downes (1978), for example, demonstrated an immediate, relatively rapid release of bound PO_4-P in water from a New Zealand lake. Shapiro et al. (1970) detected very slow "hydrolysis" in water from one Minnesota lake using progressive "hydrolysis" tests, but could not detect bound PO_4-P release in samples from 11 other Minnesota lakes (Chamberlain and Shapiro 1969). Third, are P-containing "particles" or compounds that decompose during analysis released from particulate matter into filtrates, or are P-containing "particles" normally present in lake water retained by filters? King's (1970) results, for example, suggest, but do not conclusively prove, that significant amounts of molybdate-reactive PO_4-P may be released from damaged algae, and Lean's (1976) data suggest that significant amounts of "particulate" PO_4-P in lake water may be retained by 0.45-μm filters. Answers to these questions are necessary to evaluate the accuracy of molybdenum blue measurements and to assess causes of method-specific differences in SRP determinations.

This study was undertaken specifically (1) to estimate the degree to which PO_4-P concentrations are overestimated by the Chamberlain–Shapiro (1969) isobutanol extraction method using time-course "hydrolysis" tests and to assess the effects of ammonium molybdate on release rates of bound PO_4-P, (2) to assess potential concentration-dependent effects of ammonium molybdate on SRP estimates using the extraction method and Harvey's method (Rigler 1964), and (3) to determine if filtration releases molybdate-reactive PO_4-P into filtrates or excludes P-containing particles naturally present in Lake Michigan water from filtrates. The Chamberlain–Shapiro technique has a prescribed acid exposure of 30 s and, unlike most methods, can be used for such tests because exposure times to acid or to acid plus molybdate can be varied systematically in the first step of the procedure.

Methods

LAKE WATER SAMPLES

Water was collected in October and December 1976 and during the period June–November 1977 from a depth of 4 m with a 5-L Niskin bottle at an inshore (43°04′24″N, 86°16′15″W) and an offshore (43°05′12″N, 86°25′45″W) station, 4 and 15 km west of Grand Haven, MI, respectively. Within 4–12 h, samples were filtered at a vacuum of 4.0×10^4 Pa through prerinsed (about 75 mL distilled water) 0.45-μm HA Millipore filters (47-mm diameter) into 1-L linear polyethylene bottles in a model 9-789 Fisher filtrator (Fisher Scientific Co.) fitted with a 300-mL Millipore filtration funnel. Tests on several lots of filters showed that 7.2 ± 2.0 μg P was was released from filters when 25 mL of distilled water was filtered and analyzed, but rinsing filters with a second, separate 25-mL aliquot containing 10 μg P/L as KH_2PO_4 showed that <0.1 μg P was released. Filtrates were poured into Pyrex glass jugs, stored in the dark at 5°C, and analyzed within 1–2 d. Samples were permitted to reach room temperature before analysis, and all analyses were conducted at 21 ± 1°C. Periodic tests showed that delays of up to 3 d did not result in significant changes in SRP concentrations.

ANALYTICAL METHODS

The Chamberlain–Shapiro (1969) method is a two-step extraction procedure in which phosphomolybdate is extracted into an organic solvent, excess molybdate is removed by washing the organic extract with dilute acid, and phosphomolybdate is then reduced. In the first step, a 100-mL sample was poured into a 250-mL separatory funnel, and 25 mL reagent-grade isobutanol, 5 mL 1.0% aqueous ammonium molybdate (w/v) (0.048% in sample), and 5 mL 3.3 mol/L HCl were added in that order, within 8 ± 1 s. (Acid and molybdate were forcibly injected with 5-mL auto-

matic pipettes to promote rapid mixing of reagents with the sample.) Samples were shaken immediately for 30 s and allowed to stand 60 s for phase separation; the lower (aqueous) layer was discarded within 6–8 s. In the second step, 100 mL of 0.5 mol/L HCl saturated with isobutanol was added to the organic extract, and the sample was reextracted by shaking it for 30 s, allowing it to stand 60 s for phase separation, and discarding the aqueous layer within 6–8 s. The organic layer (15–16 mL) was drained into a graduated cylinder and diluted to 25 mL with absolute ethanol. Two millilitres of a solution of 140 mg $SnCl_2 \cdot 2H_2O$/mL in 100% ethanol was added. After 9 min, optical density was measured at 650 nm in a cuvette with a 2.3-cm light path in a model II electrophotometer (Fisher Scientific Co.) or in a cuvette with a 5-cm light path in a Bausch and Lomb, model 88, spectrophotometer. Standards of known concentrations of reagent-grade KH_2PO_4 were prepared in filtered lake water and in distilled, deionized water and run in duplicate with samples. (Standards and samples for reagent and color blank determinations were split and used in all tests.)

The only deviation from the original method (Chamberlain–Shapiro 1969) was that the pH of the ammonium molybdate solution was not adjusted to pH 8.0 with NH_4OH as recommended by the authors, because tests showed that adjusted and nonadjusted solutions did not affect SRP determinations. (The pH of adjusted solutions decreased below pH 6.5 within 30 min.) The method is free of interference from silica ($Na_2SiO_3 \cdot 9H_2O$) and arsenate ($Na_2HAsO_4 \cdot 7H_2O$) at concentrations of 10 mg Si/L and 100 μg As/L and is independent of a salt effect (Tarapchak unpublished data). The detection limit was about 0.30 μg P/L using cuvettes with a 2.3-cm light path. Precision estimates (standard error of the mean), based on triplicate analyses of lake water samples in the range of 0.5–13 μg P/L, were ≤0.10 μg P/L; therefore, SRP concentrations are considered dissimilar if mean values in samples differ by >0.2 μg P/L.

Hydrolysis Tests

Time-course "hydrolysis" tests using the extraction method were conducted by two procedures: progressive "hydrolysis" tests (PHT) and shaking time tests (STT). PHT, identical with those described by Shapiro et al. (1970), were used to estimate PO_4-P release from bound sources in samples exposed to acid and to acid plus molybdate. In acid PHT, analyses were conducted by adding 5 mL of 3.3 mol/L HCl and allowing the sample to stand for time intervals ranging from "zero" (i.e. a 30-s exposure) to 12–20 min before adding isobutanol and ammonium molybdate (within ± 6 s), and extracting it by the above procedure. In acid-plus-molybdate PHT, both reagents were added simultaneously, and samples were allowed to stand for the same time intervals used in acid PHT before adding isobutanol and immediately extracting the sample. At a "zero" exposure time, samples were in contact with molybdate in acid-plus-molybdate PHT for only 2–3 s longer than in acid PHT, and samples exposed to acid in acid PHT were in contact with acid for only 5–6 s longer than in routine analysis (reagent sequence: isobutanol, molybdate, acid).

Based on the assumption that PHT might overestimate true time-0 PO_4-P concentrations if PO_4-P is released rapidly during the first 30 s (cf., Chamberlain and Shapiro 1969), shaking time tests (STT) were performed by varying exposure times in the first step of the procedure. Isobutanol, ammonium molybdate, and HCl were added successively in that order within 8 ± 1 s. Individual samples were shaken for 10, 20, 30, 40, and 60 s before allowing phase separation and then extracted as outlined above. As 5–6 s elapsed between the time that molybdate and acid were added and shaking initiated, these exposures correspond to 16, 26, 36, 46, and 66 s.

Standards and reagent and color blanks (all reagents except molybdate) were run in duplicate with samples at each exposure time. Samples were analyzed in quadruplicate, and the results averaged. Optical density of standards and reagent blanks in PHT were the same (within the limit of detection of the method) at each exposure time; therefore, increases in optical density over time in samples were attributed to release of PO_4-P from bound sources. Maximum formation of phosphomolybdate occurs by 26 s and is at least 90% complete by 16 s.

True time-0 PO_4-P values, i.e. the PO_4-P concentration in the sample immediately before reagents were added, are required for "hydrolysis" calculations. These values could not be obtained directly because samples were shaken minimally for 16 s in STT and about 30 s in PHT. Time-0 PO_4-P estimates were obtained by plotting measured SRP values vs. exposure time and extrapolating curves by eye through the y axis (Shapiro et al. 1970). Amounts of PO_4-P released into solution were calculated by subtracting time-0 estimates from time "zero" (i.e. 30-s exposures) measurements, and the percent of PO_4-P released was computed by dividing these differences by time "zero" measurements. These values are termed "minimum release estimates" because time-0 concentrations could be biased if relatively large amounts of PO_4-P were released into solution within seconds after acid reagents are added.

To determine if time-0 PO_4-P estimates approximate true PO_4-P concentrations, Rigler's (1966) radiobioassay test was performed with several STT. Fresh, unfiltered lake water was added to 250-mL Pyrex reagent bottles in an incubator maintained at in situ temperature. KH_2PO_4 was added to give concentrations ranging from 0.01 to 2.5 μg P/L, followed within 3 s by the addition of $37–185 \cdot 10^3$ Bq of carrier-free orthophosphoric acid (^{33}P-PO_4) obtained from New England Nuclear (NEN), Boston, MA. Ten-millilitre subsamples were removed within 5 s and at intervals over 2–3 h and filtered through 0.45-μm HA Millipore filters (25-mm diameter) at a vacuum of 2.7×10^4 Pa. Filters were assayed in Aquasol (NEN) in a Beckman, model LS-150, liquid scintillation counter and counts corrected for filter sorption and radioactive decay. Maximum possible PO_4-P concentrations (MPPC) were obtained by graphical analysis (Rigler 1966) and are accurate to within ±5%.

Ammonium Molybdate Effects

Potential concentration-dependent effects of molybdate on SRP concentrations were evaluated by analyzing samples using ammonium molybdate concentrations of 0.048, 0.095, 0.119, and 0.143% in the extraction method (using the prescribed sequence of reagent additions) and at concentrations

of 0.095, 0.119, and 0.143 in Harvey's method (Rigler 1964). In Harvey's method, 50-mL samples normally receive 2 mL of 2.5% ammonium molybdate (w/v) in 5 mol/L H_2SO_4 (0.095% ammonium molybdate in sample) and 0.3 mL of 0.8% $SnCl_2 \cdot 2H_2O$ (w/v) in 0.24 mol/L HCl 15–20 s later. Optical density was measured in cuvettes with a 5-cm light path 9 min after the reducing agent was added. Tests show the method to be free of interference from silica at concentrations up to 10 mg Si/L, and a salt effect biases estimates by about 20% if external rather than internal standards are used. Arsenate interferes, but does not bias determinations because total As levels at the station were <0.5 μg As/L (Eadie et al. 1979). The detection limit was about 1.0 μg P/L, and precision (standard error of the mean), based on triplicate analyses of subsamples of lake water in the range of 0.5 to 13 μg P/L, was ≤0.10 μg P/L.

Because the rate and final amount of phosphomolybdate formed are affected by the ratio of acid to molybdate concentration (Olsen 1967), standards and reagent blanks were run along with samples at each concentration. Tests showed that optical density values at ammonium molybdate concentrations used in both methods were in the acid-molybdate "plateau," and, therefore, are not biased by reduction of excess molybdate at low acid to molybdate ratios (Going and Eisenreich 1974). Phosphomolybdate formation at all molybdate levels was stable at prescribed exposure times, and optical density values of samples, standards, and reagent blanks were stable 9 min after reduction. Standards and reagent blanks were run in duplicate, and samples were analyzed in triplicate (extraction method) or quadruplicate (Harvey's method) at each molybdate concentration.

Glassware and sample bottles were scrubbed with Liquinox (Alconox, Inc., NY), a phosphate-free detergent, in hot water, soaked for 12 h or more in concentrated HNO_3, and rinsed at least six times with distilled, deionized water.

Results

Progressive Hydrolysis Tests

PHT revealed that PO_4-P in most samples was released rapidly from a bound form into solution and that ammonium molybdate accelerated release rates (Fig. 1). Three types of "hydrolysis" curves were detected. (1) Rates of PO_4-P release in subsamples exposed to acid plus molybdate were more rapid and reached higher final SRP levels than in subsamples exposed only to acid (Fig. 1A). (2) Rates in subsamples exposed to acid plus molybdate were more rapid initially than in subsamples exposed to acid, but SRP concentrations at longer exposure times in acid treatments were equal to or approached values obtained from acid-plus-molybdate exposures (Fig. 1B). (3) SRP concentrations remained constant at shorter exposure times, but increased at one of the longer exposure times (Fig. 1C). Minimum PO_4-P release in acid and acid-plus-molybdate exposures overestimated time-0 PO_4-P concentrations by 0–86% and by 0–81%, respectively (Table 1).

SRP values in most samples were highly dependent on small variations in exposure time, and "hydrolysis" curves reveal that calculated PO_4-P release values are underestimated by PHT. Values from time "zero" (i.e. 30-s exposure) acid-plus-molybdate treatments often were substantially higher than values obtained from time "zero" acid treatments. Inspection of Table 1 clearly shows that both of these time "zero" estimates often were substantially higher than SRP measured by routine 30-s analysis based on the prescribed

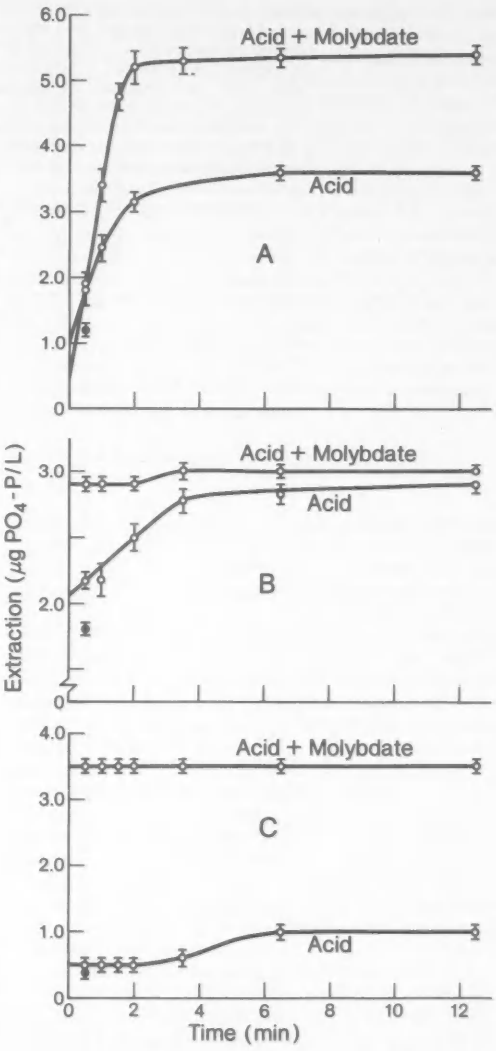

FIG. 1. Progressive "hydrolysis" tests, based on variations in exposure time to acid and acid plus molybdate in the first step of the Chamberlain–Shapiro extraction method, on filtered samples of water collected from a depth of 4 m in southern Lake Michigan. Solid circles are SRP values obtained by using the prescribed sequence of reagent additions. A, Inshore station, June 3, 1977. B, Inshore station, June 12, 1977. C, Offshore station, June 12, 1977. Precision of SRP estimation is shown as the standard error of the mean (vertical bars).

TABLE 1. Results of progressive "hydrolysis" tests, based on acid (first row) and acid-plus-molybdate (second row) exposure in the Chamberlain–Shapiro extraction method, on filtered water from a depth of 4 m from an inshore and an offshore station in southern Lake Michigan. Time-0 PO_4-P estimates were obtained by extrapolation; time-"zero" (30 s*) estimates are based on exposure to acid (reagent sequence: acid, isobutanol, molybdate) and to acid plus molybdate (reagent sequence: acid plus molybdate, isobutanol); and SRP estimates obtained by using the prescribed exposure time (30 s**) and reagent sequence (isobutanol, molybdate, acid). Percent minimum PO_4-P release is calculated by subtracting the time-0 estimate from the 30-s* estimate and dividing by the 30-s* estimate.

	Exposure time			
Date	Time-0 estimate	30-s* measurement	30-s** measurement	Minimum release
		μg PO_4-P/L		
Inshore				
June 3, 1977	1.0	1.8		44%
			1.2	
	0.4	1.9		79%
June 12, 1977	2.1	2.2		5%
			1.8	
	2.9	2.9		0%
July 11, 1977	1.4	1.4		0%
			1.3	
	1.2	1.6		25%
Aug. 17, 1977	0.4	0.8		50%
			≤0.3	
	0.8	1.1		27%
Sept. 22, 1977	0.8	1.2		33%
			0.8	
	0.5	2.7		81%
Oct. 20, 1977	4.7	4.9		4%
			3.0	
	3.8	4.5		16%
Offshore				
Oct. 22, 1976	0.1	0.7		86%
			≤0.3	
	—	—		
Dec. 15, 1976	1.2	1.2		0%
			1.2	
	—	—		
June 12, 1977	0.5	0.5		0%
			≤0.3	
	3.5	3.5		0%
July 13, 1977	0.8	1.1		27%
			0.6	
	2.0	2.0		0%
Aug. 19, 1977	1.6	1.6		0%
			1.3	
	2.0	2.1		5%
Sept. 21, 1977	2.8	3.5		20%
			2.0	
	4.1	4.6		11%
Oct. 21, 1977	5.6	6.0		7%
			4.2	
	4.7	5.2		10%

sequence of reagent additions (Table 1; shown as black circles in Fig. 1). These differences, relative to routine 30-s analysis, are produced by a discrepancy of only several seconds in contact time with acid and with molybdate in the presence of acid, and are readily apparent in Fig. 1C (see also Fig. 1B). Note that PO_4-P release was not detected during the first 2 min, but that SRP measured after the time "zero" acid-plus-molybdate exposure was seven times higher than the time "zero" estimate from acid PHT. Calculations of PO_4-P release (Table 1) therefore underestimate the true percentage of PO_4-P released into solution during the first 30 s because acid and acid-plus-molybdate PHT elevate bound PO_4-P release rates. If curves from acid and acid-plus-molybdate PHT are extrapolated using measurements from routine 30-s analysis as time "zero" concentrations (see Fig. 1A), they will intersect the *y* axis much nearer the origin. Extrapolation

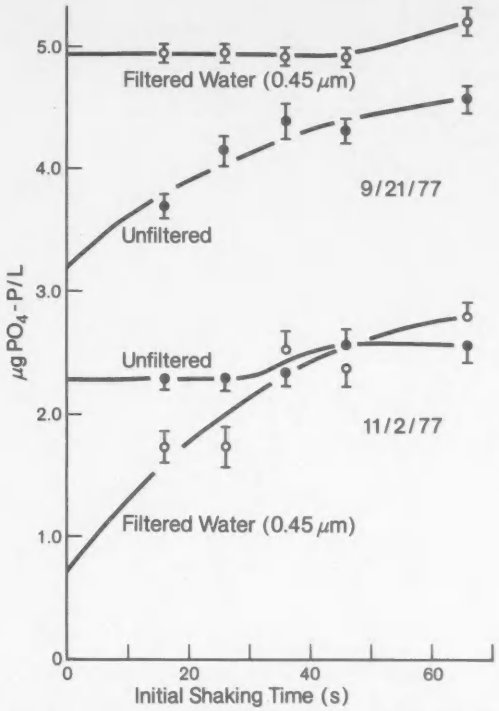

FIG. 2. Shaking time tests, based on variations in exposure time to acid molybdate in the first step of the Chamberlain–Shapiro extraction method, on samples of filtered and unfiltered water collected from a depth of 4 m at an offshore station in southern Lake Michigan. Precision of SRP estimation is shown as the standard error of the mean (vertical bars).

of PHT curves through the *y* axis, therefore, overestimates time-0 PO_4-P concentrations and only yields estimates of minimum PO_4-P release rates.

SHAKING-TIME TESTS, COMPARISONS OF MAXIMUM POSSIBLE PO_4-P CONCENTRATIONS AND TIME-0 PO_4-P ESTIMATES, AND FILTRATION ARTIFACTS

Two types of "hydrolysis" curves were detected in seven STT: (1) SRP increased as exposure times were increased, and (2) SRP remained constant at shorter exposure times, but increased at one or more of the longer shaking times, (cf., Fig. 2). Substantially lower SRP values generally were obtained by shaking samples for 16 instead of 36 s, and estimates of minimum PO_4-P release showed that time-0 PO_4-P concentrations were overestimated by up to 72%.

Four of these STT also were performed to investigate filtration artifacts by comparing "hydrolysis" curves in filtered vs. unfiltered samples (Fig. 2). Filtration of the November 2 sample apparently removed highly acid-labile "particles" that were hydrolyzed in the first 16 s because SRP measured at exposures of 16 and 26 s were lower in the filtrate than in the unfiltered sample. Filtration of the September 21 sample showed that acid-labile "particles" were removed during filtration because PO_4-P release occurred in unfiltered water, but "hydrolysis" apparently did not occur in the filtrate between 16 and 46 s. Filtration also must have resulted in a release of PO_4-P or acid-labile compounds or "particles" from algae or from abiotic "particulate" sources into the filtrate because SRP concentrations were higher in the filtrate.

Three comparative analyses using STT and Rigler's (1966) method were performed to determine if time-0 PO_4-P values overestimated maximum possible PO_4-P concentrations (MPPC). MPPC in samples of unfiltered water collected on September 21, September 22, and November 2 were 0.2, 0.3, and 0.1 μg P/L, respectively, and time-0 PO_4-P estimates were 3.2, 3.2, and 2.3 μg P/L, respectively, showing that PO_4-P was released very rapidly between true time-0 and the 16-s exposure and that true time-0 PO_4-P concentrations were overestimated minimally by at least an order of magnitude. (See Discussion and Conclusions.)

EFFECTS OF MOLYBDATE CONCENTRATIONS ON SRP MEASUREMENTS

Concentration-dependent effects of ammonium molybdate on SRP determinations were apparent in most samples (Table 2). SRP values sometimes were below detection limits at low molybdate concentrations and frequently varied two- to three-fold or more between the lowest and highest molybdate levels. In over one-half of the samples tested by the extraction method, values measured at a molybdate level of 0.095% were different from values obtained by using the prescribed molybdate concentration (0.048%). Differences in SRP concentrations measured by Harvey's method were not as pronounced. In many samples, values measured at molybdate concentrations of 0.119% were not dissimilar from those detected at the prescribed concentration (0.095%).

Three tests were performed to determine if molybdate-reactive PO_4-P was released from "particulate" matter in filtrates or if P-containing "particles" were excluded from filtrates. Unfiltered water and a subsample filtered through 0.45- and then serially through 0.22- and 0.10-μm membrane filters were analyzed by both methods. SRP values at all molybdate levels generally were higher in unfiltered than in filtered water; concentrations generally were lower in subsamples that had been refiltered through filters of smaller pore size, and values generally increased as successively higher molybdate concentrations were used (Table 3). Similar results, showing up to eight-fold variations in SRP concentrations in 0.45- vs. 0.10-μm filtrates, were detected in the two other tests, demonstrating that large amounts of bound PO_4-P were released from "particles" between 0.45 and 0.10 μm in filtrates.

Discussion and Conclusions

Several conclusions regarding the accuracy of SRP estimation, PO_4-P concentrations, and the chemical composition of the molybdate-reactive PO_4-P pool can be drawn from our tests. True PO_4-P concentrations are overestimated by the Chamberlain–Shapiro extraction method and Harvey's method (Table 2) and cannot be accurately approximated by

TABLE 2. Concentration-dependent effects of ammonium molybdate on SRP determinations measured by the Chamberlain–Shapiro extraction method (first row) and Harvey's method (second row) on filtered samples of water collected from a depth of 4 m at an inshore (In) and an offshore (Off) station in southern Lake Michigan. Prescribed ammonium molybdate concentrations are 0.048% (extraction method) and 0.095% (Harvey's method).

Date	Station	% molybdate concentration			
		0.048	0.095	0.119	0.143
			μg PO_4-P/L		
June 12, 1977	In	1.7	2.3	3.5	4.0
			2.7	2.7	2.9
June 12, 1977	Off	≤0.3	0.6	1.0	1.6
			1.0	1.5	1.9
July 11, 1977	In	1.3	2.4	2.7	2.6
			2.1	2.5	2.7
July 13, 1977	Off	0.6	2.3	2.6	3.0
			2.3	2.3	3.1
Aug. 17, 1977	In	≤0.3	3.5	3.4	3.9
			1.9	2.3	2.6
Aug. 19, 1977	Off	1.3	1.3	1.6	1.6
			2.8	3.3	3.6
Sept. 21, 1977	Off	2.1	2.9	3.2	6.6
			5.4	5.4	5.8
Sept. 22, 1977	In	0.8	2.2	2.4	2.6
			4.7	5.2	5.2
Oct. 20, 1977	In	2.9	3.2	3.2	3.6
			5.1	5.0	5.6
Oct. 21, 1977	Off	4.2	4.9	4.8	5.1
			2.3	2.6	3.1

TABLE 3. Concentration-dependent effects of ammonium molybdate on SRP determinations measured by the Chamberlain–Shapiro extraction method (top row) and Harvey's method (bottom row) in a sample of unfiltered water collected on August 19, 1977, from an offshore station in southern Lake Michigan and in subsamples filtered through 0.45-, 0.22-, and 0.10-μm membrane filters. Prescribed ammonium molybdate concentrations are 0.048% (extraction method) and 0.095% (Harvey's method).

Sample	% ammonium molybdate concentration			
	0.048	0.095	0.119	0.143
		μg PO_4-P/L		
Unfiltered	2.3	2.2	3.7	5.6
		4.4	4.7	5.9
0.45 μm	1.3	1.3	1.6	1.7
		2.9	3.2	3.5
0.22 μm	≤0.3	0.8	1.5	1.5
		1.4	1.9	2.1
0.10 μm	≤0.3	0.6	0.7	0.7
		≤1.0	1.1	1.3

PHT or STT. Extremely rapid release of bound PO_4-P can be illustrated indirectly by noting that time-"zero" (i.e. 30 s) exposure to acid and to acid-plus-molybdate differ by only 2–3 s in molybdate contact time (Fig. 1C)! Rigler (1966) indicated that maximum possible PO_4-P concentrations (MPPC) usually are one to two orders of magnitude lower than SRP values; therefore, routine 30-s SRP measurements and most time-0 PO_4-P estimates from PHT (Table 1) grossly exaggerate true time-0 PO_4-P concentrations. Two important methodological implications stem from these results. (1) Substantially different SRP values can be obtained simply by varying the length of time samples are exposed to acid molybdate or by using different molybdate concentrations. The range of SRP values obtained for any one sample by simply varying molybdate concentrations (Table 2) can, in fact, account for the entire range of method-specific discrepancies noted by many investigators (cf., Jones 1966; Jones and Spencer 1963). (2) Methods based on short exposures, e.g. the 6-s method of Chamberlain and Shapiro (1969), or further attempts to modify conventional molybdenum blue methodology by decreasing acid contact time, will not avoid "hydrolysis" in water from Lake Michigan or in other lakes if the bound PO_4-P pool is highly labile to acid molybdate.

The accuracy of SRP estimation also can be affected by filtration artifacts (Fig. 2; Table 2). Claims that algae rupture and leak molybdate-reactive PO_4-P into filtrates are based

primarily on analogy with the apparent loss of ^{14}C-labeled material from algae during filtration (cf., Rigler 1973). Nalewajko and Lean (1972) demonstrated, however, that evidence for ^{14}C loss from cells can be an artifact caused by retention of ^{14}C compounds by membrane filters. Similarly, King's (1970) attempts to demonstrate leakage of molybdate-reactive P from algae are inconclusive because ^{32}P-PO_4, rather than direct measurements of SRP, was used to detect PO_4-P loss, and the results are complicated by sorption of the isotope by filters. STT on Lake Michigan water demonstrate that molybdate-reactive PO_4-P can be released from particulate material (September 21) and that retention of P-containing "particles" by filters also can occur (November 2) (Fig. 2). Other tests on water from these stations clearly show that up to 50% of the SRP in unfiltered lake water can be removed by filtration through 0.45-μm membrane filters, and that leakage of molybdate-reactive PO_4-P from algae or by fragmentation of particulate material during filtration can account for up to one-half of the SRP detected in 0.45-μm filtrates (Tarapchak unpublished data). These artifacts are variable and will depend on the density of P-containing "particles" in lake water, the rate at which filter pores clog with debris, and the amount of stored PO_4-P contained in microorganisms and their susceptibility to damage during filtration.

Rates of bound PO_4-P release in Lake Michigan water appear to be far more rapid than those reported in other investigations. Shapiro et al. (1970) detected relatively slow "hydrolysis" in an acid-plus-molybdate PHT in water from Linwood Lake, Minnesota, that overestimated the routine 30-s SRP measurement by about 20%. Paerl and Downes (1978) demonstrated that a molecule of high molecular weight (>5000) constituted the bulk of the SRP pool in filtered water from Lake Tutaeinanga, New Zealand. "Hydrolysis" tests using reagents from the ascorbic acid method (Strickland and Parsons 1972) and the 6-s method of Chamberlain and Shapiro (1969) gave release rates comparable to the November 2 filtered sample (Fig. 2). In contrast, Chamberlain and Shapiro (1969) failed to detect "hydrolysis" between 30-s and 15-min exposures in PHT in water from 11 Minnesota lakes, and concluded either that acid-labile compounds were not present or that PO_4-P was completely released before the 30-s measurement. Our analyses suggest that the second explanation may have been correct. Bound PO_4-P can be completely released after a 16-s exposure and time-0 PO_4-P values can overestimate MPPC by an order of magnitude (Fig. 2, see above). Moreover, our results show that Harvey's method also grossly overestimated true PO_4-P concentrations because SRP estimates were comparable to those obtained by the extraction method (Table 2). These results agree with a recent study by Stainton (1980). He demonstrated that colloids (molecular size 100–5000) in 0.45-μm membrane-filtered water from Lake 227 in the Experimental Lakes Area, Ontario, Canada, released large amounts of PO_4-P when subjected to reagents of five molybdenum blue methods (including Harvey's method and the Chamberlain–Shapiro extraction method). Consequently, all conventional molybdenum blue methods must be viewed as an unsatisfactory means of measuring true PO_4-P concentrations in lake water.

Acceleration of acid "hydrolysis" rates in Lake Michigan water by ammonium molybdate (Fig. 1) is dramatic and has never been reported for lake waters. The mechanism by which molybdate "catalyzes" release of bound PO_4-P is unknown, but could involve one or more of the following processes. (1) Molybdate may catalyze acid hydrolysis of dissolved organic compounds. Such compounds, however, probably do not represent a major source of SRP (see below). (2) Molybdate may accelerate the rate at which PO_4-P is released from "particles" in filtered lake water. Such particles may contain an organic PO_4-P component, e.g. metallorganic complexes (cf., Riger 1973; Chamberlain and Shapiro 1973) that undergo acid hydrolysis more rapidly in the presence of molybdate. (3) Addition of ammonium molybdate to filtrates may displace PO_4-P from "particles" by competing with PO_4-P for charged sites or by disrupting the PO_4-P equilibrium between the "particulate" and the dissolved pool.

The chemical composition of the SRP pool in lake water is not well known (Rigler 1973). Our tests demonstrate that major changes in the molybdate-reactive PO_4-P pool must have occurred during the study period: PO_4-P was released at different rates by exposure to acid and acid plus molybdate and the ratio of SRP obtained from acid and acid-plus-molybdate exposures varied, and the concentration-dependent effects of molybdate on SRP determinations were dissimilar (Tables 1 and 2). Variations in SRP detected by PHT were unrelated to changes in water temperature, pH, or alkalinity and probably represent biologically mediated transformations of the SRP pool. Moreover, most of molybdate-reactive PO_4-P in filtrates must come primarily from "particles." Data in Table 2 and other analysis on water from these stations demonstrate that 80% or more of the SRP and at least 90% of the ^{33}P-PO_4 in 0.45-μm filtrates can be removed by refiltration through 0.10-μm membrane filters (Tarapchak unpublished data). Although release of PO_4-P from dissolved organic compounds cannot be completely ruled out, two arguments suggest that this pool does not represent a significant SRP source. Refiltration of 0.45-μm filtrates through smaller filters should not reduce SRP concentrations, and the average lability and relative concentrations of organic compounds in lake water are low (Chamberlain and Shapiro 1973). Our data, coupled with Chamberlain's (1968) work and molecular size fractionation studies of Paerl and Downes (1978) and Stainton (1980), suggest that most of the SRP in lake water filtrates is "particulate."

Potential sources of "particulate" PO_4-P in Lake Michigan filtrates could include large organic molecules or their fragments (cf., Minear 1972), colloidal inorganic–organic complexes including humic materials (cf., Olsen 1967; Francko and Heath 1979), or capsular or fibrillar material produced by microorganisms (cf., Paerl and Lean 1976; Lean 1976). Although calcium carbonate particles, colloidal iron phosphate, or silts and clays can release PO_4-P during analysis (Olsen 1967; Golterman 1973), they would be effectively removed from lake water by 0.45-μm membrane filtration. Previous studies and some of our results suggest that PO_4-P may have been released primarily from a single pool. Stainton's (1980) results and those of Paerl and Downes (1978) demonstrate that PO_4-P was released largely from a single pool. "Hydrolysis" curves from some tests (cf., Fig. 1A, Fig. 2: September 21 unfiltered water, November 2 filtered water) suggest that PO_4-P also was released from a single bound pool because the data fit a first-order hydrolysis model relatively well. Evidence for PO_4-P release from two or more pools, however,

was observed in several tests (cf., Fig. 2: September 21 unfiltered water; November 2 unfiltered water; Fig. 1C acid exposure). PO_4-P must have been released from one or more pools before the 16- or 30-s exposure. Another pool apparently released PO_4-P abruptly at one of the longer exposure times, suggesting that dissolution or a slow desorption process occurred. Further analyses clearly are necessary to determine more precisely the chemical composition of the SRP pool in lake water and the mechanisms by which bound PO_4-P is released when acid molybdate is added.

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Fish Abundance and Distribution Near Three Heated Effluents to Lake Michigan[1]

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SPIGARELLI, S. A., R. M. GOLDSTEIN, W. PREPEJCHAL, AND M. M. THOMMES. 1982. Fish abundance and distribution near three heated effluents to Lake Michigan. Can. J. Fish. Aquat. Sci. 39: 305–315.

A combined echo location–temperature mapping technique was used to determine the abundance and distribution of fish with depth and temperature in locally heated and unheated areas of Lake Michigan. Surveys were conducted between April and October at two adjacent power plants in the southern basin and at one plant in the northern basin of the lake. Fish densities in plume and reference areas differed seasonally. Densities typically differed by a factor of 2–4 although on one occasion plume area density was 90 times greater. Highest plume densities occurred during late spring when alewife (*Alosa pseudoharengus*) were spawning inshore. Consistently dense congregations of fish were found downstream of the interfaces between ambient shore-parallel currents and discharge flows. The general distribution of fish with depth was similar in all areas. Differences between plume and reference areas were related to the discharge type: at canal discharges fish tended to congregate inshore while at the offshore discharge they congregated in deeper zones. Fish also tended to occupy shallower depth strata in all plume areas. Positive correlation between fish density and increasing temperature was common at both plume and reference areas during all three seasons, but more frequent at plume areas. Temperatures selected by fish in plume areas were 1–3°C higher than maximum ambient temperatures.

Key words: fish distribution, thermal outfall, temperature, depth, discharge type, Lake Michigan

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En vue de déterminer l'abondance et la distribution des poissons en fonction de la profondeur et de la température dans des zones réchauffées localement et non réchauffées du lac Michigan, nous avons fait appel à une technique combinée d'écho–location et de graphiques des températures. Des relevés ont été effectués entre avril et octobre à deux centrales électriques voisines dans le bassin sud et à une autre dans le bassin nord du lac. La densité des poissons dans les zones de « panaches » et de référence diffère selon la saison. Les densités diffèrent typiquement d'un facteur de 2–4, bien qu'en une occasion, la densité dans les zones de panaches étaient de 90 fois supérieure. Les densités maximales dans les panaches sont observées à la fin du printemps, quand le gaspareau (*Alosa pseudoharengus*) est en train de pondre près du rivage. On observe des rassemblements de poissons toujours denses en aval de la surface de contact entre les courants ambiants parallèles au rivage et le débit des effluents. La distribution générale des poissons en fonction de la profondeur est semblable dans toutes les zones. Les différences entre les zones de panaches et de référence sont liées au type d'émissaire : à l'émissaire des canaux, les poissons tendent à se rassembler près du rivage, alors qu'à l'émissaire du large, les poissons se rassemblent dans les zones plus profondes. Les poissons tendent également à occuper des couches de profondeurs moindres dans toutes les zones de panaches. La corrélation positive entre la densité des poissons et une température ascendante est commune, tant dans les zones de panaches que dans les zones de référence, aux trois saisons, mais plus fréquente dans les zones de panaches. Les températures

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choisies par les poissons dans les zones de panaches sont de 1 à 3°C plus élevées que les températures ambiantes maximales.

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PERIODIC attraction or avoidance responses by fish have been indicated by field studies at power plant discharges to lakes, streams, and estuaries. In most cases, trawls, gill nets, or electroshockers were used to sample fish and to compare relative abundances between heated and unheated areas. Species diversity and relative abundance of some species apparently are altered in thermally enriched areas (e.g. Gammon 1973; McErlean et al. 1973; Neill and Magnuson 1974; Romberg et al. 1974).

A growing number of researchers are extolling the advantages of hydroacoustic techniques over conventional methods of determining fish distribution and abundance near water intakes and discharges (e.g. Spigarelli et al. 1973; Thomas 1979). Kelso and Minns (1975) used hydroacoustic techniques to investigate the summer distribution of fish near a thermal effluent to Lake Ontario and concluded that there was little difference in the distribution or temperature selection of fish between heated and unheated areas. Studies using conventional sampling methods at power plant sites on Lake Michigan typically have indicated that fish are attracted to thermal effluents, but the sampling methods were unsuitable for quantitative analysis of fish distribution. Through the combined use of thermal plume mapping and acoustic "sampling" of fish we have investigated fish responses to three power plant discharges into Lake Michigan. This nondestructive technique allows rapid observation of fish distribution patterns and provides data that can be used to compare temperature selection, depth selection, numbers, and biomass of fish in heated and unheated areas.

The consequences of temperature-induced changes in fish distribution and abundance are unclear, but numerous hypotheses have been advanced; e.g. (1) altered predator/prey ratios leading to shifts in trophic pathways and transfer rates of energy and materials; (2) changes in migratory patterns and reproductive success; and (3) the creation of local "oases" or "deserts." To assess or predict these and other effects, accurate estimates of the magnitude of changes and the factors influencing changes must be obtained.

Sampling Methods

Three-dimensional temperature profiles were measured using a gunwale-mounted thermistor array coupled to data acquisition (DAS) and positioning systems (Van Loon et al. 1977). Information from these systems was processed by computer to produce maps of temperature as a function of position in both the horizontal and vertical planes. The computer-produced maps of the vertical plane temperature data (0−3 m) were used to transfer the temperature information to the sonar recordings as 1°C isotherms.

The acoustic fish locating system has a range of 0−91.4 m, a frequency of 105 kHz, and a pulse width of 0.6 ms. Deployed just below the water's surface on a vehicle towed ahead of the vessel, the 22° transducer was directed vertically downward. In operational mode, the recorder chart was indexed at intervals with clock time and the present coordinates from the positioning system.

Using the sonar recorder as a guide, 2- to 3-km transects were run at a constant depth and speed (~2.5 m/s), roughly paralleling the shore along depth contours. Transects of the plume areas were continued until the DAS readout indicated continuous ambient temperatures. Transects of similar lengths were sampled in the unheated reference areas (upcurrent from the thermal source). Typically, surveys (plume plus reference) were conducted between 09:00 and 15:00. Turbulence and air entrainment near the discharge points precluded discrimination of fish echos in the warmest plume regions; wave-entrained air occasionally obscured the surface regions in all areas. The obscured volumes were not included in any analyses.

Echo data from each sampling date were recorded graphically and on magnetic tape. In all cases discrimination between fish echos and echos caused by entrained air in specified areas was a significant problem. Attempts to use a sophisticated computer technique (image processor) and an electronic technique (signal digitizer) failed because air bubble "noise" was not uniformly distributed and could not be located or eliminated without case-specific human decision and programming. Echo-integration techniques were explored, but these were rejected for the same reason. Consequently, all of the graphically recorded echos were counted manually by one individual. Manual recounts of many data sets showed high reproducibility with variations of less than 10%.

For statistical comparisons, transects along depth contours were divided into subsections (cells) of equal length (occasional unequal cell lengths were taken to avoid recording density = 0). Individual fish echos were counted in each cell, depth zone, and temperature region. The volumes sampled and densities of fish in each subvolume were calculated based on water column depth, the beam angle of the transducer, and the length of the cell.

Thomas (1979) stated that "biological variability accounts for a large portion of the error observed in most (hydroacoustic) estimates of the nearshore fish density." This was anticipated in our study, as we restricted our sampling to a common daylight period and to physically similar areas. Other sources of error in estimation (e.g. target strength and echo-sounder gain characteristics) have been studied more recently (Thorne 1978), but it is apparent that careful sampling design is the most important consideration in minimization of error.

Site Descriptions

POINT BEACH NUCLEAR POWER PLANT

Located on the west shore of Lake Michigan (Two Creeks, Wisconsin), this plant consists of two 500 MW pressurized water reactors. The intake structure is 530 m offshore

and discharge water is returned to the lake through two 10.7-m-wide discharge flumes extending 50 m offshore. The flumes angle 30° from the plant centerline, discharging in northeasterly and southeasterly directions. At full power, average discharge velocity is ~0.5 m/s, flow is 45 m^3/s, and the temperature increase across the condensers is ~10.7°C.

The focus of the "400 m radius," an arbitrary area used to define the near-field plume region, was at the shore on the centerline between the two discharge flumes. The two reference regions were located 6 km south and 4 km north of the plant, respectively.

Zion Nuclear Power Station

The Zion facility located at Zion, Illinois (205 km south of the Point Beach Plant), consists of two pressurized water reactors having a combined capacity of 2200 MW. The cooling water intake is a submerged pipe located 730 m offshore. The two high-velocity diffuser discharges are submerged (3.6 m) and located 230 m offshore and 47 m on either side of the plant centerline. Each discharge has two ports angling 45° away from the plant centerline and from the shore. Under maximum load the discharge velocity is ~2.9 m/s, flow is ~97 m^3/s, and the temperature rise is ~11°C.

The focus of the 400-m radius was along the plant centerline and between the two discharge structures. A reference area located north of the Zion plant was used for both the Waukegan and Zion sites. A second reference area 4 km south of the Zion site also was used on occasion.

Waukegan Generating Station

Located at Waukegan, Illinois, 8 km south of the Zion station, this seven-unit fossil-fueled plant has a gross capacity of 1100 MW. At maximum capacity, the condenser cooling water flow is ~55 m^3/s, discharge velocity is ~2 m/s, and the temperature rise is ~7°C.

The parallel shoreline intake and discharge canals are separated by a 175-m-long breakwater angled in a southeasterly direction. The focus of the 400-m radius was the center of the discharge canal at the shoreline. The region is bounded by the extension of the breakwater on the south and the northern shoreline. The reference region for this plant was the north reference for the Zion plant.

Data Analysis

Spatial Distribution and Abundance

The total extent of the transects and the volumes of water sampled by echo location were defined as total plume and total reference areas, i.e. the total plume area contained heated discharge water (the true plume), the interface between heated and ambient water, and an ambient zone at the periphery of each transect. Thus, comparisons between plume and reference areas were not strict comparisons between heated and unheated areas. To ensure that conditions created by the discharge would not be obscured by inclusion of ambient conditions, a second region was defined for each plume area which included all sections of transects within a 400-m radius of a discharge. As the direction of plumes varied depending on prevailing currents and winds, the 400-m circle was bisected into northern and southern halves.

Three sets of comparisons were used to characterize the spatial distribution of fishes about these thermal discharges. The first set compared overall densities (number of fish observed/volume of water sampled) within plume and reference areas. The second set compared the north and south halves of the 400-m areas. The third set investigated abundance in the entire water column at specific bottom depths (vertical sections) and abundance within depth strata (horizontal sections). Because of the large temporal variation in observed densities (three orders of magnitude), the nonparametric Wilcoxon Sign Rank Test was applied for most comparisons.

Prior to instituting more rigorous statistical analyses, the distributions of fish density were tested with the Kolmogorov–Smirnov test for normality and in every case were shown to be non-normal. Logarithmic and square root transformations were applied and values of skewness, kurtosis, and variance were examined to determine the appropriate transformation. Based on these inspections, the log-transformed data were selected as best conforming to a normal distribution.

Depth and Temperature Selection Analysis

The influences of depth and temperature on fish distribution were analyzed by determining the slopes of linear regressions between log-transformed fish density and transect depth or temperature. Analysis of variance was used to test for differences in density. The linear and nonlinear components of total variance were calculated and tested to confirm the linearity of responses. The linear components of variance as determined from each regression were summed and compared to the summed error variances. The resulting ratio follows an F distribution and can be used to test the significance of the linear component of total residual errors from the analyses of variance. The linear component of variance accounted for greater than 90% of the total variance ($F = 33.95$; df = 44, 13377; $P < 0.0005$) for depth; and ~80% for temperature ($F = 15.05$; df = 40, 2263; $P < 0.005$). Thus, depth and temperature selection were defined and compared on a relative scale by determining the slopes of linear regressions. The magnitude and sign of the slope were used as indices of strength and direction of the selection response. A two-way classification (plume or reference × season) analysis of variance was applied to test for differences using the slopes of the regressions as variables weighted by the variance of the density observations for each site and day.

The distribution of fish with temperature was used to determine selected temperatures, i.e. between the 1°C isotherms where the greatest (modal) density of fish was observed. Selected temperatures at plume and reference areas were compared to each other and to preferred, selected, and avoidance temperatures of Lake Michigan species.

Results and Discussion

Spatial Distribution and Abundance

Comparisons of fish densities in plume and reference areas

TABLE 1. Densities of fish (No./10 000 m^3) observed within thermal plume (P) and reference (R) regions.

Date	Area[a]	Total P	Total R	400 m[b] P	400 m[b] R	Plume 400 m North	Plume 400 m South	Ambient current[a]
Spring								
Apr. 17, 1974	Z	30	25	21	42	15	28	V
Apr. 17, 1974	W	32	25	29	30	44	18	N/A
Apr. 25, 1974	P	24	28	84	49	103	65	N
May 21, 1974	P	318	522	494	1274	738	286	N
May 23, 1974	Z	279	71	56	70	28	88	V
May 23, 1974	W	156	71	217	123	232	205	N
June 14, 1973	P	183	2	2866	5	5169	1533	N
June 18, 1974	P	392	159	4388	578	796	7784	S
June 20, 1974	Z	308	272	724	959	334	1149	S
June 20, 1974	W	107	75	595	1312	973	292	N
Summer								
July 30, 1974	P	15	26	189	108	70	310	S
Aug. 1, 1974	Z	60	41	256	103	120	412	S
Aug. 1, 1974	W	37	41	82	119	113	49	N
Aug. 3, 1973	P	57	57	78	208	55	105	V
Aug. 16, 1973	P	4	12	8	15	9	7	N
Sept. 4, 1974	P	17	25	70	83	24	118	S
Sept. 10, 1974	Z	29	36	48	60	49	47	S
Sept. 10, 1974	W	24	36	31	74	55	7	S
Sept. 28, 1973	P	23	68	264	174	531	70	S
Fall								
Oct. 10, 1974	P	22	231	72	1185	57	86	N
Oct. 23, 1973	P	3	4	9	16	15	0	V

[a]P = Point Beach; Z = Zion; W = Waukegan; N = north; S = south; V = variable direction.
[b]No statistical comparisons were made. Underlined values are significantly higher ($P < 0.05$).

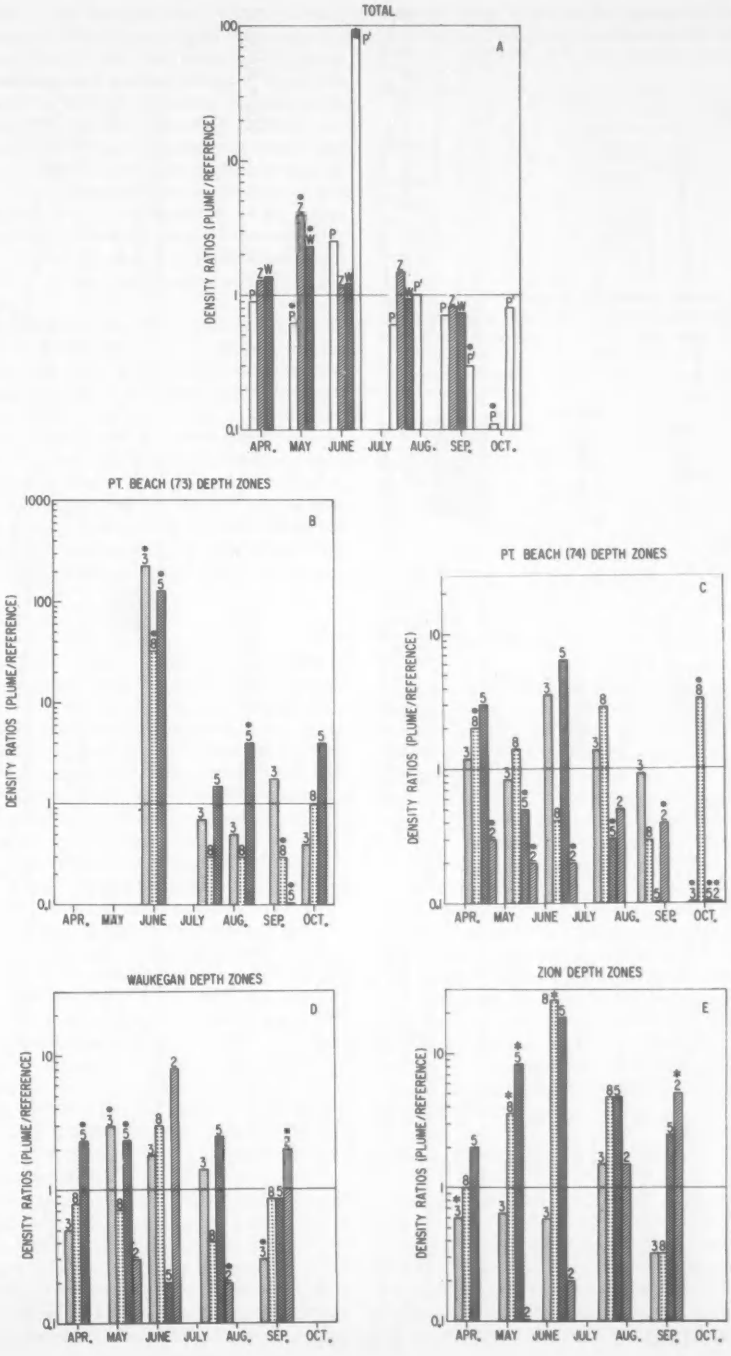
showed very large seasonal differences within and between areas. These extreme variations precluded detection of annual differences in fish densities between plume and reference areas (all data pooled). Nonparametric comparisons showed that mean area densities were not statistically different ($P > 0.1$) and site-specific linear regressions of plume vs. reference densities resulted in slopes that were not significantly different from unity. On 9 out of 21 sampling dates plume area densities exceeded reference area densities and on three occasions plume area densities were significantly higher ($P < 0.05$). Significantly higher densities were also observed in reference areas on three occasions (Table 1 and Fig. 1A). These comparisons indicate a tendency for fish to congregate in these heated areas in May and June, but not in early spring, midsummer, or early fall. The magnitude of "attraction" or "avoidance," as shown by the density ratios in Fig. 1A, was quite variable between survey dates at each site. At Point Beach the ratio ranged between 91 and 0.1; i.e. nearly a two-order magnitude "attraction" in June 1973, and an order of magnitude "avoidance" in October 1974. It is likely that large temporal variations occur at most power plant sites as fish respond to short-term (e.g. upwellings) and long-term changes in temperature and other important factors controlling their distribution.

Alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) are the most abundant species in these areas, as indicated by fish impingement data from the three power plants (Spigarelli et al. 1981). At least 98% of the total numbers of fish impinged each month at Zion (1974) were alewife and smelt, and these two species typically comprised >90% of the monthly impingement totals at Waukegan and Point Beach. Smelt spawn inshore during early spring and relatively high impingement densities were observed in April (adults) and in the fall when the young of the year (YOY) were abundant inshore. Alewife migrate inshore in late spring and typically spawn between May and July. Densities of impinged alewife are highest between May and July with secondary peaks in October when the YOY are abundant inshore. Thus, the apparent pattern of fish congregation in thermal plumes coincides with the major alewife spawning period (May–June) at each site.

In a similar study on Lake Ontario, Kelso and Minns (1975) concluded that alewife and smelt selected pelagic areas rather than interacting with the "nearshore fish community." Because their study spanned the period between July and October, the results tend to confirm previous observations that both species move offshore after spawning; but their study did not describe fish behavior during the spawning periods.

Densities of fish were usually greater ($P < 0.05$) within the 400-m radii of the discharges than within total plume areas,

FIG. 1. Ratios of fish densities in plume and reference areas. (A) Total area ratios. (B–E) Density ratios in depth zones at each site. 2 = 2–3 m; 3 = 3–5 m; 5 = 5–8 m; 8 = >8 m; starred ratios indicate statistical difference ($P < 0.05$) between plume and reference densities. Z = Zion; W = Waukegan; P = Point Beach 1974; P′ = Point Beach 1973.


TOTAL
A
DENSITY RATIOS (PLUME/REFERENCE)
100
10
1
0.1
APR. MAY JUNE JULY AUG. SEP. OCT.
PT. BEACH (73) DEPTH ZONES
B
1000
PT. BEACH (74) DEPTH ZONES
C
WAUKEGAN DEPTH ZONES
D
ZION DEPTH ZONES
E

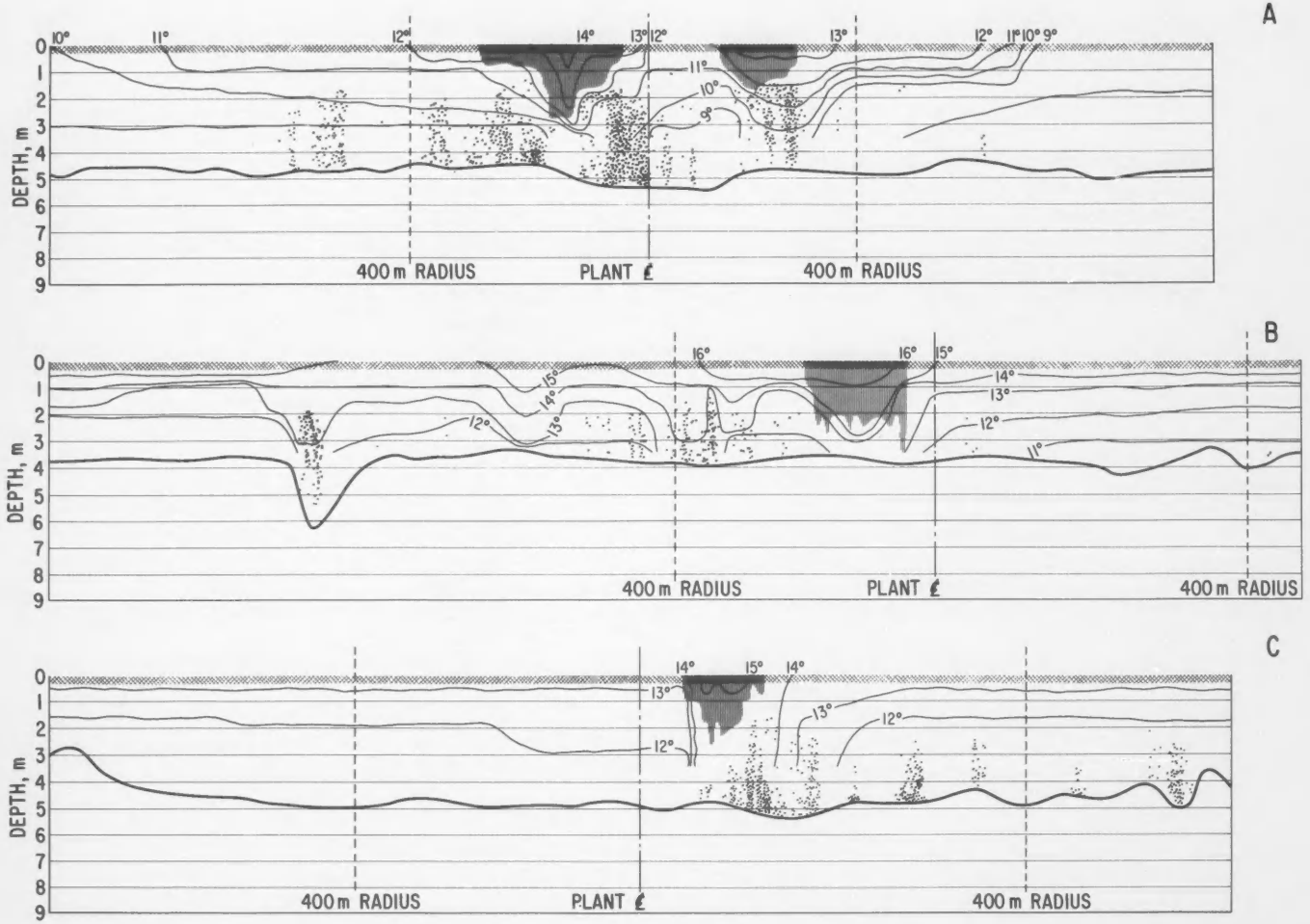


FIG. 2. Graphic renditions of example echograms showing tendency of fish to congregate in downcurrent regions of plumes. A = Point Beach, June 18, 1974, 5 m; B = Waukegan, June 20, 1974, 4 m; C = Zion, June 20, 1974, 5 m (shaded areas = turbulent plume).

but these nearfield plume densities were not consistently greater than densities of fish observed in an equivalent area and volume at the reference area. Comparisons of fish densities between the northern and southern halves of the 400-m radii in plumes indicated 10-fold differences on some dates. Fish tended to congregate on the downcurrent (ambient current) side of the discharge or below the turbulent plume waters prior to September. Figure 2 shows an example of this response from each site. Slopes of linear regressions of fish densities in downcurrent vs. upcurrent halves of the 400-m radii over the entire study period and prior to September were both significantly greater than unity ($P < 0.05$). Coefficients of determination (R^2) for these regressions were 0.70 and 0.76, respectively.

Strong currents parallel to shore (>0.1 m/s) create a well-defined, abrupt zone of temperature change on the upcurrent side of the discharge and a more gradual temperature gradient on the downcurrent side. The downcurrent side of the plume may be preferred by adult smelt and alewife as the response was prevalent when these fishes predominated the inshore community. Such a response could be related to (1) the general positive rheotaxis exhibited by alewife (Romberg et al. 1974; Richkus 1975), and the tendency for both species to be anadromous; (2) a feeding benefit derived from "fallout" of entrained organisms in plume water; or (3) an avoidance of the abrupt thermal gradient on the upcurrent side of the plume.

Depth Distribution

The distributions of fish within transect depth zones (vertical sections) were not consistently different between plume and reference areas (Fig. 1). In most cases, at least one of the sampled zones near the canal discharge at Point Beach showed a density ratio >1, indicating increased density compared to that of the reference area. Thus, on any given day, one or more of the plume depth zones probably contains a congregation of fish while the other zones are depleted in density relative to the reference area. A similar set of responses (ratios) was observed at the Waukegan site (Fig. 1D) which also utilizes a canal discharge. On all sampling dates at least one depth zone contained an apparent or statistically higher density of fish than comparable reference zones.

The patterns of density ratios at the Zion site (offshore diffuser) were different from those at the two canal discharges (Fig. 1E). At Zion, fish tended to congregate in the 5–8 and >8-m depth zones, and avoided the shallower zones. The Zion discharges are located between the 3- and 4-m contours, and the high-velocity diffusers may cause fish to avoid the shallower depths (except during September when the 2- to 3-m contours were preferred over all depths). Also, higher density ratios (5–25) were observed each month at the diffuser, compared to typical ratios of ≤3 at Waukegan and Point Beach (canal discharges).

Fish density also tended to decrease with increasing depth stratum (horizontal layer) in all areas. The general linear decrease in density with depth in the water column was variable among seasons. During spring the intermediate strata (3–8 m) were preferred in plume areas, but in reference areas fish tended to congregate in shallower strata. During summer and fall the reverse occurred as the mid-depths were avoided in plume areas, and fish tended to congregate in shallower strata.

TABLE 2. Mean slopes of the regressions between fish density (logarithm) and water depth by area and season. (Differences between areas are significant, $P < 0.05$; between seasons nonsignificant, $P > 0.05$.)

	Area	
Season	Plume	Reference
Spring	−0.356	−0.576
Summer	−0.344	−0.488
Fall	−0.480	−0.520
Combined	−0.367	−0.529

TABLE 3. Mean slopes of regressions between fish density (logarithm) and temperature by area and season. (Differences between seasons are significant, $P < 0.05$; between areas nonsignificant, $P > 0.05$.)

	Area		
Season	Plume	Reference	Combined
Spring	0.58	0.70	0.63
Summer	0.22	0.80	0.42
Fall	0.50	1.03	0.88

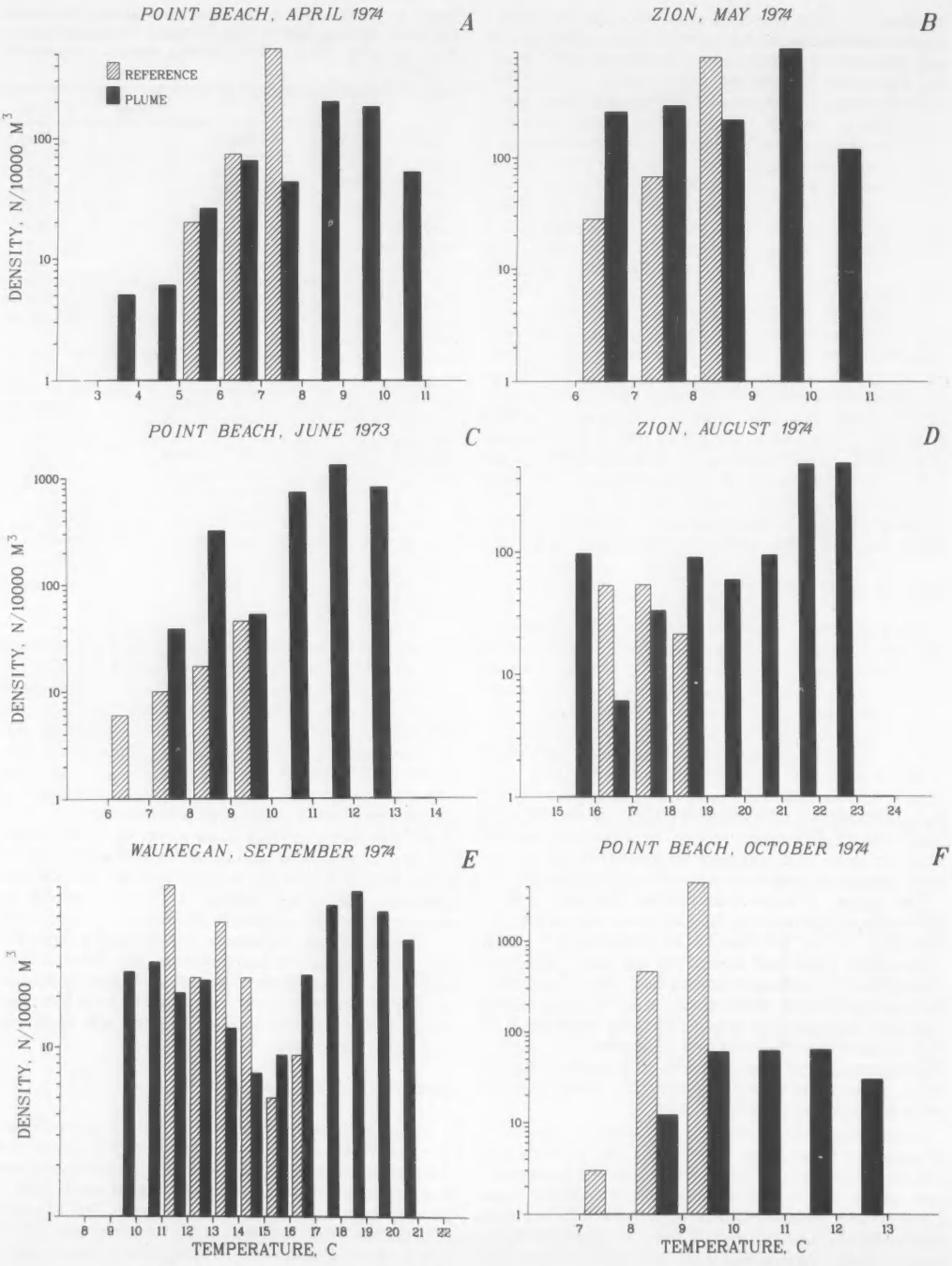
Depth Selection

On all but two sampling dates the density of fish decreased with increasing depth zone. The frequency of significant regressions was almost equal at plume and reference areas (≈86%) and increased with seasonal progression, i.e. 72, 94, and 100% in spring, summer, and fall, respectively. Regressions tended to be consistently significant or nonsignificant for both plume and reference areas on the same day. This indicates that thermal discharges do not reverse general trends in fish selection of depth zones.

The analysis of variance of the slopes of the regressions indicated no significant seasonal differences in the way fish density correlated with increasing depth (Table 2). However, there was a significant difference ($P < 0.05$) between the magnitude of depth selection at plume and reference areas, i.e. the decrease in fish density with increasing depth was more pronounced at the reference areas. The slopes of these regressions and the results of the statistical analyses indicate that fish are more abundant inshore than offshore at both types of areas, but the natural distribution of fish with depth was modified in plume areas.

Temperature Selection

Temperature selection occurred at both plume and reference areas during all seasons, but the slopes of the regressions of log-transformed fish density with temperature for each date were not all significant or positive. On approximately 10% of the sampling dates the response was negative. The frequency of significant correlations was greater at plume areas (75%) than at reference areas (44%). The analysis of variance indi-


POINT BEACH, APRIL 1974
A
REFERENCE
PLUME
DENSITY, N/10000 M3
ZION, MAY 1974
B
POINT BEACH, JUNE 1973
C
ZION, AUGUST 1974
D
WAUKEGAN, SEPTEMBER 1974
E
POINT BEACH, OCTOBER 1974
F
TEMPERATURE, C
TEMPERATURE, C

cated that the magnitude of the temperature selection response differed with season ($P < 0.05$), but not between areas ($P > 0.1$). Temperature selection, regardless of area, was strongest during fall and weakest during summer (Table 3). The magnitude of the temperature selection response may depend on the number of temperature zones available. At the reference areas fish were limited to fewer temperature zones and any degree of positive temperature selection produced a skewed distribution resulting in a high selection response (magnitude of slope). The slopes of density-temperature regressions (Table 3) were of smaller magnitude than the slopes of those between density and bottom depth (Table 2).

Typically, modal (selected) temperatures were at the upper end of the temperature ranges sampled in reference areas and 0−5° higher in plume areas (Fig. 3). Between April and June, the density of fish in both heated and unheated areas increased with temperature up to single selected temperatures (Fig. 3A−C). Later in summer the temperatures sampled at plume areas extended both above and below the range of temperatures found at the reference areas, and the distributions tended to be bimodal (Fig. 3D). The bimodal thermal distribution of fish was most pronounced in September samples as the number of temperature zones increased to a maximum of 12 (Fig. 3E). In October the density distributions at the Point Beach plume and reference areas were similar to spring distributions (Fig. 3F).

Bimodal distributions of fish with temperature may be explained by the availability of large temperature ranges which include the preferred or optimum temperatures of more than one species or age-class. Brandt et al. (1980) hypothesized that Lake Michigan forage species and age-groups within species may reduce competition for food by thermal segregation. In September he found YOY alewife at epilimnial temperatures greater than 15° (most at 17−19°), adult alewife at thermocline temperatures of 11−14°, and adult smelt at 7−18° with peak abundance at 7−8°. Wells (1968) reported the upper avoidance temperatures to be 22° and 14° for alewife and smelt, respectively, in Lake Michigan.

The thermal distribution of fish near Point Beach in April (Fig. 3A) may reflect temperature selection by smelt as the reference (7−8°) and plume (8−10°) modes correspond to smelt selection reported by Brandt et al. (1980). In June, the development of bimodal distributions in plumes (Fig. 3C) indicates the presence of fish with different thermal preferences or acclimations. Density maxima occurred near the highest temperatures sampled in both plume and reference areas, but these distributions may not be indicative of temperature selection by alewife as higher temperatures were available (but not sampled) in plumes. The bimodal

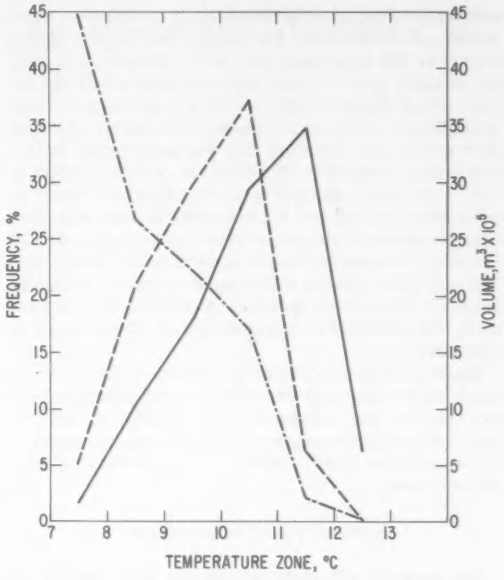


FIG. 4. Frequency distributions of fish (numbers) in temperature zones (Point Beach, June 1974) based on the observed densities (—) and on extrapolation to total volumes (---). Total volumes at each temperature (·-·-·).

distributions observed in August and September (Fig. 3D, E) may reflect the relative abundance of smelt and alewife as well as of adult and juvenile fishes. The upper avoidance temperature of smelt (14°) as determined by Wells (1968) coincides with the density minima in September at each site. Density modes at lower temperatures probably represent temperatures selected by smelt. In October, the ratio of smelt to alewife impinged at Point Beach is reversed from previous months and typically exceeds 2−3 (Spigarelli et al. 1981). The observed density distribution at this site (Fig. 3F) may indicate segregation betweeen YOY smelt (reference) and YOY alewife (plume).

TOTAL ABUNDANCE AND DISTRIBUTION

Although relatively high densities of fish were observed within certain isotherms, it is probable that, as a result of the limited volumes of water at those temperatures, the total

TABLE 4. Numbers of fish at Point Beach plume and reference areas (June 1974) derived by isotherm and transect density methods.

	Plume area	Reference area	Ratio
Temperature-based estimate	752 330	193 396	3.9
Transect-based estimate	225 334	92 691	2.4
Ratio	3.3	2.1	

FIG. 3. Distributions of fish density with temperature in plume and reference areas, selected to show seasonal changes in fish responses.

numbers of fish may be greater at other temperatures where volumes are much greater. For example, two frequency distributions of fish with temperature were developed, one using the numbers of fish in sampled temperature zones and the other which estimated total numbers in temperature zones throughout the plume area. Comparison of the two frequency distributions (Fig. 4) showed they were quite similar, but the peaks were offset by ~1°C. Estimates of total numbers of fish in the plume and reference areas based on density at temperature and adjusted for isothermal volumes were 2–3 times greater than estimates based on average transect density (Table 4). The apparent controlling factor is the uneven distribution of water volumes at different temperatures. Estimates based on transect density values do not take this into account and could lead to underestimates of fish abundance in either area.

Figure 4 is instructive in that the frequency distribution of fish is shown relative to the volume–temperature plot. Both the observed and extrapolated fish distributions indicate selection of temperature zones with relatively low volumes, i.e. congregation of fish into low volume–intermediate temperature zones.

Summary and Implications

The results of this study indicate that large numbers of alewife congregate near and within thermal plumes during the spawning period (May and June), but that adult smelt and YOY of both species are not strongly attracted to heated discharges between April and October. Very large differences were observed in the densities of fish between the north and south sides of nearfield plume areas prior to September, i.e. dense congregations of fish consistently were found downstream of the interfaces between ambient currents and discharge flows. Depth contour and stratum selection was modified in plume areas as fish tended to congregate more inshore near canal discharges and toward the surface at all discharges compared to reference areas. Fish in plume areas selected higher temperatures than those in reference areas and thermal segregations of species and/or size-classes (bimodal distributions) were apparent in heated areas with wide temperature ranges.

The densities of fish in plume areas can exceed densities in reference areas by two orders of magnitude during late spring and early summer while reference area densities may exceed plume area densities by a factor of 10 in late summer and early fall. These responses indicate that adult alewife are attracted to the thermal and/or flow characteristics of the discharges during spawning season, but not during other seasons.

Large differences in forage fish abundance and subtle differences in their distribution between heated and ambient temperature waters may not be of great significance to forage fish populations, assuming no direct effects result from the changes (one possibility is an increase in alewife impingement due to the attractive nature of the heated discharge during the spawning period). Large numbers of predatory salmonids also orient to thermal discharges, residing in heated waters for days at a time and acclimating to temperatures 3–10°C above ambient (Spigarelli and Thommes 1979). When inshore densities of forage are low and mean plume densities are even lower, the energetic costs of plume-residence by salmonids may be severe. However, the relatively high densities of forage fishes in certain zones (e.g. downcurrent, nearfield plume) may be sufficiently high to attract salmonids and to offset the energy demands associated with plume residence (W. K. Derickson et al., Int. Soc. Ecol. Modelling, Int. Symp. Energy Ecol. Modelling, April 20–23, 1981, unpublished data).

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Behavioral Interactions and Body Size Differences in Competition for Food among Juvenile Brown Bullhead (*Ictalurus nebulosus*)

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KEEN, W. H. 1982. Behavioral interactions and body size differences in competition for food among juvenile brown bullhead (*Ictalurus nebulosus*). Can. J. Fish. Aquat. Sci. 39: 316–320.

The effects of relative body size (larger or smaller fish), absolute body size differences, food level, and social interactions on the growth rates of juvenile brown bullhead (*Ictalurus nebulosus*) catfish were determined for pairs of fish. Overall growth rate of the larger fish was higher than for the smaller fish, although this difference did not depend on absolute body size difference within pairs. The reduced growth rates of both larger and smaller fish at limited food level was independent of both relative size difference and absolute body size difference within pairs. Both larger and smaller fish had highly variable growth rates. Size dominance and aggression were common within many pairs, yet this behavior was unrelated to food level and absolute body size difference. Aggression within pairs was not diminished by adding structural complexity to simple environments. It is suggested that the high variability in growth rates was due to differences in individuals within pairs with respect to the intensity of behavioral interactions. Social interactions within pairs of fish were apparently unrelated to food level and were strong enough to mask both exploitative and interference mechanisms which may have been functional in competition for limited food.

Key words: body size, dominance hierarchies, exploitation competition, food level, *Ictalurus nebulosus*, interference competition, behavioral interactions

KEEN, W. H. 1982. Behavioral interactions and body size differences in competition for food among juvenile brown bullhead (*Ictalurus nebulosus*). Can. J. Fish. Aquat. Sci. 39: 316–320.

Les effets de la taille corporelle relative (poissons grands ou petits), des différences de taille corporelle absolue, du niveau trophique et des interactions sociales sur les taux de croissance de jeunes barbues de rivière (*Ictalurus nebulosus*) ont été déterminés sur des paires de poissons. Le taux de croissance général des grands poissons est plus rapide que celui des petits, bien que cette différence ne dépende pas d'une différence de taille corporelle absolue au sein de mêmes paires. Les taux de croissance réduits des grands aussi bien que des petits poissons à des niveaux trophiques limités sont indépendants à la fois des différences de taille relative et des différences de taille absolue au sein de mêmes paires. Les grands et les petits poissons ont tous des taux de croissance très variables. Parmi plusieurs paires, la dominance et l'agression liées à la taille sont communes, sans que ce comportement soit en relation avec le niveau trophique et avec la différence de taille corporelle absolue. L'addition d'une complexité structurale à des environnements simples n'atténue pas l'agression parmi les paires. Nous suggérons que la forte variabilité des taux de croissance est due à des différences entre individus de mêmes paires sous le rapport de l'intensité des interactions comportementales. Les interactions sociales au sein des paires ne semblent pas liées au niveau trophique et sont suffisamment fortes pour masquer les mécanismes tant d'exploitation que d'interférence possiblement fonctionnels dans la compétition pour une nourriture limitée.

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BODY size is one of the primary factors determining the outcome of intra- or inter-specific competition between animals for limited food resources (Wilson 1975), and it has been verified in many laboratory studies that larger body size confers a competitive advantage in groups of fish (Brett 1979). The phenomenon of growth depensation, in which variability in body size increases with time within groups, is generally known from fish studies. Growth depensation may often be the result of larger animals acquiring greater quantities of a limited food resource (Yamagishi 1969).

Various mechanisms facilitate the greater use of food by larger fish. Larger fish may compete more successfully for limited food because they can consume a wider range of food

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particle sizes, or prey items, than smaller ones (Wankowski and Thorpe 1979; Magnuson 1962), and larger fish will be able to consume a disproportionate quantity of food when it is available. Behavioral mechanisms in some cases facilitate the acquisition of food by larger fish through interference with the smaller members of a population. Size-based dominance hierarchies and territoriality are the two common interference mechanisms in competition (Morse 1974; Brown and Orians 1970).

Types of social organization within groups of fish, such as size dominance hierarchies, do not always operate as mechanisms in competition for food (Brett 1979). However, they have been known to influence the growth rates of fish in two ways. First, some species develop dominance hierarchies at restricted food levels which suppress growth of the smaller fish, but the effect of this dominance is absent or greatly diminished when food is not limited (Magnuson 1962; Nagoshi 1967a, b). Such a pattern is clearly indicative of interference competition for limited food. In the second pattern, the dominant individuals exert a negative influence on growth of subordinates at all levels of food resource (Yamagishi et al. 1974), and intraspecific aggression does not diminish with increasing food levels. These social interactions are thus apparently not directly related to food gathering. Among sexually mature fish, the existence of this second pattern is likely to be related to reproductive activities; however, the bases for such behavior in juvenile fish are not apparent.

Although competition for food and mates is well known among fishes, other critical resources in the environment may be the direct objects of competition. Shelter objects may serve as the centers of territories, and thus initially, space or quality of habitat may be the focus of interference interactions (Kodric-Brown 1978; Bardach and Todd 1970).

The primary purpose of this study was to determine if body size differences and dominance hierarchies are important mechanisms in competition for food among groups of juvenile brown bullhead (*Ictalurus nebulosus*). A second purpose was to determine if adding structural complexity to the environment would lead to diminished aggression within pairs of fish.

Experimental Procedure

Fish for the experiments were collected by seining from a small lake in southern Onondaga County, New York. All specimens were collected on June 2 and were kept until used in the laboratory in 135-L aquaria at densities of about one fish/L. Temperature of the room ranged from 21 to 24°C. Fish used in the experiments were sexually immature and ranged in size from 3.6 to 17.6 g. Age of the fish was from 9 to 11 mo, as determined from observation of growth rings in otoliths of a random sample of 17 fish used in experiments.

Size dominance hierarchies were established within small groups of *I. nebulosus* held in the laboratory; therefore body size or behavioral dominance may serve as exploitative or interference mechanisms in acquiring food resources. The first experiment was performed to determine the effects of body size difference, food level, and behavioral interactions on growth rate. Pairs of fish were arranged in a three-way factorial design with four absolute size differences within pairs (factor A), three food levels (B), a relative size difference (larger or smaller) within pairs (C), and four replicates of each combination of the three factors.

Seven of the 48 tanks were dropped from the experiment because one fish of the pair died. The absolute size differences within pairs were <1, 2–3, 5–6, and 8–9 g, and food levels were 2, 4, and 6% of initial wet fish weight per day. For pairs which had <1-g size difference, the left nasal barbel of the larger fish was clipped so that individuals could be recognized. Clipped barbels began regeneration quickly and the loss of this barbel is not likely to have had any influence on the fish. The tanks were arranged randomly around laboratory tables and cardboard strips were used to separate the tanks to prevent possible visible communication between fish in different tanks. The natural photoperiod prevailed, with light reaching the tanks only indirectly from windows at each end of the room. Tanks were 32 × 17 × 19 cm aquaria with covers, containing 6 L of water and were aerated lightly through airstones. Water was changed at the same time in all tanks every 3rd or 4th day. The food used was trout chow (Strike®, AgWay, Inc.) which was finely ground and sieved, and then mixed with one part (by mass) gelatin to 2.5 parts water to 4.8 parts ground food. The prepared food was chopped into small particles (1–3 mm), weighed, and kept refrigerated until used. Fish were fed once daily between 16:00 and 19:00 and the experiment was run for 28 d. Fish were reweighed after the first 14 d and food quantities for the second half of the experiment were adjusted to fish weight at that time.

Fish were weighed and paired according to absolute size difference and no effort was made to control the range of sizes. Growth rates of fish are not constant over all body sizes (Brett 1979); however, the small range of body sizes used in this experiment, and the uniformity of age of the fish, gave some assurance that size-specific growth rates were not an important factor. Data were recorded as percent wet weight gain per gram of fish from initial weight. Weight gains were all less than 30%, and were transformed for statistical analyses to arcsin $\sqrt{p}$ (Steel and Torrie 1980), where p is the percent weight gain per gram of initial fish weight. Fish were also observed daily for fin damage and injuries which may have been caused by intraspecific aggression.

In sexually mature groups of *I. nebulosus* (Breder 1935, 1939) and the closely related *I. natalis* (Bardach and Todd 1970), individuals establish territories around objects in their environments, and such territories probably result in diminishing intraspecific aggression. The second experiment was conducted to determine if aggression observed within pairs of fish was related to the simplicity of the environment in the tanks. This experiment was initiated on July 19, in the same 48 tanks as the first experiment. A clay pot with 10 cm open top was placed on its side in alternate tanks to serve as cover, and two fish were placed in each tank. The fish were weighed in pairs, and not individually, although pairs were chosen so that a larger and smaller fish could be determined by observation. These pairs were fed 4% of their initial body weight per day and other conditions were as described for the first experiment. Incidence of injuries due to aggressive encounters within the 48 pairs of fish was observed for a 14-d period.

Results

The three-way analysis of variance (Table 1) indicated that the growth rate of smaller and larger fish was different, and

TABLE 1. Analysis of variance of percent weight gain with respect to absolute body size difference within pairs of fish, food level, and relative body size difference (larger or smaller fish). Data were transformed to arcsin $\sqrt{p}$ for analysis; p = percent of weight gain over initial body weight. df = degrees of freedom. (**$P < 0.001$; * $P < 0.05$.)

Source of variation	df	Mean square	F
Absolute body size difference (A)	3	68.45	2.38[a]
Food level (B)	2	433.27	15.04**
Relative body size (C)	1	142.56	4.95*
Interaction			
A × B	6	44.83	1.56[a]
A × C	3	15.58	0.54[a]
B × C	2	53.50	1.86[a]
A × B × C	5	23.45	0.81[a]
Error	59	28.80	

[a]Not significant.

that food level had an important influence on growth rate. The absolute body size difference, however, had no influence on growth rate, and there were no important interactions between any of the three factors.

Overall, the smaller fish of the pairs grew at a slower rate than the larger ones (Tables 1, 2). Food level influenced weight gain of smaller fish (Table 2) as the mean growth of fish fed 2% of their wet weight was less than those fed 6%, but was not different from the 4% group. Although the absolute weight difference within pairs had no important influence on growth rates, the differences in average weight gain of the smaller fish were more than twofold over the range of absolute body size differences of the larger fish (Table 2). There was, therefore, considerable variability in weight gains of the smaller fish at all levels of size difference of paired fish. The lack of interaction between food level and body size difference indicates that the differential growth due to food level was independent of the absolute body size difference within pairs.

Food level also influenced weight gains of the larger fish, with gains at 2% food level being different from both 4 and 6% levels (Table 2). Larger fish, like the smaller, had no differences among weight gains with respect to size difference of pairs. The magnitude of difference in mean weight gain for the larger fish with respect to absolute size difference was, however, considerably less than for the smaller fish. As there was no interaction between food level and absolute body size difference, the effect on the larger fish due to food level was apparently independent of absolute body size difference within pairs.

Behavioral dominance based primarily on body size developed in many of the pairs. The aggression within pairs, mostly noticeable in nipping at the caudal fin by the dominant fish, often resulted in injuries to the subordinate animal (Table 3). Injuries seemed to appear randomly over the time period, some occurring within the 1st day and others late in the experiment. Injuries were noted for one member of a pair in 24 tanks, and although only three of the larger fish were injured (Table 3), during the test period seven fish died, all of which were the smaller of a pair.

The severity and incidence of aggression were not clearly related to either food level or magnitude of size difference (Table 3); four of the seven fish that died were in the 2% food level group, and this tendency may be an indication of important differences in survival at low food levels. In spite of the clear size dominance in the overall experiment, aggression as measured by injuries to fish was not as severe in the 8- to 9-g size difference pairs. The two intermediate size difference groups had the most injuries. The 17 injured fish remaining at the end of the experiment actually had a higher mean weight gain (16.6%) than the dominant fish with which they were paired (14.6%), although this difference was not significant ($P > 0.40$).

The incidence of injuries to fish was independent of the presence or absence of a cover object (Table 4) ($P > 0.75$). Adding a cover object to the simple environments did not diminish aggressive encounters. Smaller fish were injured

TABLE 2. Mean weight gain (as percent of initial weight) for (a) the smaller, and (b) the larger of paired fish over the 28-d experimental period. Mean ($\bar{x}$) and standard error (SE) of the mean for weight gain are listed for each size difference and food level.

Food level	Weight difference (g) between paired fish				
	<1	2–3	5–6	8–9	$\bar{x}$ (SE)
			(a) Small fish		
2%	5.9	9.0	3.0	6.7	6.9 (1.81)[a]
4%	13.9	21.0	8.8	9.5	14.1 (2.31)[a]
6%	19.3	14.3	20.2	5.6	14.9 (2.33)[a]
$\bar{x}$ (SE)	13.9 (2.97)	15.4 (2.74)	12.9 (2.69)	7.32 (2.08)	
			(b) Large fish		
2%	10.3	7.3	4.5	4.6	6.7 (1.77)[b]
4%	17.9	24.6	23.9	16.5	20.3 (2.16)[b]
6%	21.2	15.8	22.5	18.3	19.7 (1.86)[b]
$\bar{x}$ (SE)	17.0 (2.34)	16.7 (2.99)	16.8 (4.10)	13.9 (2.70)	

[a]Mean weight gain at 2% food level was significantly different from that at 6% ($P < 0.05$), but not at the 4% level ($P > 0.05$) by Student–Newman–Kuels' test.

[b]Mean weight gain at 2% food level was significantly different from that at both 4 and 6% ($P < 0.01$).

TABLE 3. Number of fish having observable injuries due to aggressive encounters within pairs during the 28-d experimental period. All but three of the injured fish were the smaller of the pair.

Food level	Weight difference (g) between paired fish				Total	
	<1	2–3	5–6	8–9	Injured	Deaths
2%	2[a,b]	1[a]	3[a]	3[a]	9	4
4%	1	3[b]	2[a,a]	1	7	2
6%	1	4[a,b]	2	1	8	1
Total injured	4	8	7	5		
Total deaths	1	2	3	1		

[a]Indicates smaller fish of one pair died.
[b]Indicates larger fish of one pair was injured.

more frequently than larger fish ($P < 0.01$), as in the previous experiment.

Discussion

When social organization is not of major importance, larger body size generally facilitates the more efficient exploitation of a limited food resource and is thus an important factor in the growth rates of individual fish within groups (Brett 1979). The overall growth rate of larger individuals within pairs of juvenile *I. nebulosus* was higher than for the smaller fish, although the absolute body size difference within pairs was not important. If effective exploitative competition for food were operating through absolute body size difference, then evidence in the form of differential growth rates would have been especially likely under conditions of limited food. Both the larger and smaller members of pairs had lower, and approximately the same, growth rates at limiting food level (2%). There was some indication of greater exploitative capability in food gathering by the larger fish when the size difference was large (8–9 g), as the average growth rate of the larger fish was almost twice as high as for the smaller fish at this size difference. This difference, however, was not significant. Exploitative competition for food based on absolute body size difference was not an important process in juvenile *I. nebulosus*.

Aggression and size dominance, as they exist among juvenile *I. nebulosus*, could operate as mechanisms to facilitate the acquisition of greater quantities of a scarce food resource by dominant individuals. If limited food supply induces agression and dominance, then this behavioral pattern would be expected to diminish when food was not limited. The incidence of aggression in *I. nebulosus* was not related to level of food resources — the incidence of injured fish was about equal at all food levels. This pattern of aggression, irrespective of food level in *I. nebulosus*, is similar to that observed by Yamagishi et al. (1974) in the goby (*Odontobutis obscurus*). The evolution and maintenance of such a behavioral pattern are apparently related to factors other than competition for food.

A clearly defined dominance relationship was established within many pairs of *I. nebulosus* based primarily on body size, with 21 of 24 cases of injury in the first experiment being to the smaller fish. The actual intensity of aggressive encounters was not, however, related to magnitude of size difference. Because dominance by the larger fish was not absolute, and because the intensity of aggressive encounters did not appear to exhibit any pattern with respect to food level or magnitude of body size difference, the tendency toward aggression must have been quite variable and characteristic of the individuals. Prior history of the individual is important in determining aggressive tendencies in juvenile Atlantic salmon (*Salmo salar*) (Keenleyside and Yamamoto 1962; Fenderson and Carpenter 1971). Variability in growth rates and behavioral tendencies may also be attributable to genetic differences (Magnuson 1962).

TABLE 4. Number of fish receiving observable injuries due to aggression within pairs over a 14-d experimental period when a cover object was present or absent.

Cover object	Fish	
	Smaller	Larger
Present	10[a]	2
Absent	7[a]	2

[a]Two smaller fish died in tanks with the cover object present and two died in tanks without cover.

The dominance established within pairs apparently affected growth rates of individual fish differently; overall growth rate of the larger fish was higher than that of the smaller fish. Growth rate, however, was highly variable for both larger and smaller fish. The energy requirement for maintaining a dominance relationship may be highly variable for the dominant as well as subordinate fish, depending on the intensity and frequency of conflicts. In a small group of gobies (*O. obscurus*) the first ranking subordinate surpassed the dominant fish in growth due to a lower level of food intake and less efficient food/growth conversion by the dominant fish (Yamagishi et al. 1974). Rubenstein (1981) also found for the Everglades pygmy sunfish (*Elassoma evergladei*) that individuals holding territories or winning aggressive encounters in dominance hierarchies did not benefit by greater growth. The high variability in weight gains observed in *I. nebulosus* may have been due to different energy demands within pairs resulting from intensity of conflict, and the growth of both larger and smaller fish may have been somewhat suppressed where conflict was great.

Competition for space, not directly related to food resources, may induce the aggressive encounters observed in juvenile *I. nebulosus*. Kodric-Brown (1978) found that the optimal habitats for establishment of breeding territories by male pupfish (*Cyprinodon* sp.) were those with greater topo-

graphic diversity, and that introduction of objects into simple habitats facilitated establishment of territories. In the medaka *Oryzias latipes*, Magnuson (1962) found that the magnitude of aggression was diminished as environmental complexity increased. Introduciton of a cover object did not, however, diminish the aggressive encounters among juvenile *I. nebulosus*. The requirement for adequate space and environmental diversity for resolving aggressive conflicts may still have been lacking in these experimental tanks.

Ictalurus nebulosus is primarily a nocturnal forager, with benthic organisms comprising the largest proportion of its diet (Trautman 1955; Klarberg and Benson 1975); during daylight hours most individuals are inactive and under cover. The intraspecific aggression and size hierarchies observed among the sexually immature individuals used in this study may be adaptive in facilitating the acquisition and retention of shelter or cover objects by larger fish. The social interactions observed here are retained in sexually mature *I. nebulosus* (Breder 1935, 1939), at which time the behavior serves functions related to reproduction. Intraspecific aggression among juvenile *I. nebulosus* does not appear to be functional in either exploitative or interference competition for food. If competition for food occurs at all, it is apparently based on the greater exploitative capability of larger body size in consuming food. With variable food particle size, more efficient exploitation by larger individuals would be facilitated. The social organization and behavior within small groups of juvenile *I. nebulosus* are of great importance, yet they are not directly related to acquisition of food. This study confirms that, in addition to food resource level, the characteristic social organization within groups of fish is an important determinant of growth rates (Brett 1979).

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Difficulties in Aging Atlantic Salmon (*Salmo salar*) and Brown Trout (*Salmo trutta*) from Cold Rivers Due to Lack of Scales as Yearlings

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JENSEN, A. J., AND B. O. JOHNSEN. 1982. Difficulties in aging Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) from cold rivers due to lack of scales as yearlings. Can. J. Fish. Aquat. Sci. 39: 321 – 325.

Scales in Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) from two cold Norwegian rivers first appeared when the salmon were 33–34 mm long (total length) and the trout were 35–38 mm long. A considerable proportion of the yearlings did not form scales in years with a low water temperature (less than 1000–1100 degree-days from May to October); these individuals lacked the first annulus in the scales. Scales with five circuli or more seldom occurred. The number of days per year with a water temperature above 6.5°C was better correlated to the formation of scales in Atlantic salmon than the degree-days. In years when the water temperature exceeded 6.5°C for more than 70–80 days, only minor errors arose in age determination of the salmon; when the temperature exceeded 6.5°C for less than 70–80 days, some individuals lacked the first annulus in their scales.

Key words: Atlantic salmon, brown trout, age determination, temperature, scale formation

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Chez les saumons atlantiques et les truites brunes de deux cours d'eau norvégiens froids, les écailles apparaissent pour la première fois à des longueurs totales de 33–34 mm et 35–38 mm respectivement. Dans les années où l'eau est froide (moins de 1000–1100 degrés-jours entre mai et octobre), une forte proportion des poissons d'un an n'ont pas encore formé d'écailles; chez ces poissons, le premier annulus manque sur les écailles. On ne rencontre que rarement des écailles à cinq circuli ou davantage. Dans la formation des écailles du saumon atlantique, il y a meilleure corrélation entre le nombre de jours par année où la température est supérieure à 6,5°C qu'avec le nombre de degrés-jours. Dans les années où la température de l'eau dépasse 6,5°C pendant plus de 70–80 jours, on ne trouve que des erreurs mineures dans la détermination des âges; quand la température dépasse 6,5°C pendant moins de 70–80 jours, les écailles de certains sujets sont dépourvues d'un premier annulus.

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FROM experiments with artificially reared fry of Atlantic salmon (*Salmo salar*), Dannevig (1928) pointed out the possibility that very slow growing individuals do not form scales the first summer. Sømme (1941) was aware that in scales of brown trout (*Salmo trutta*) from Norwegian mountain lakes, the first very small annulus may be situated only three to four circuli from the center of the scale. The same is known from the highlands of Scotland (Frost and Brown 1967). In Lake Øvre Heimdalsvatn, a Norwegian mountain lake, Jensen (1977) often found a very narrow annulus in scales of brown trout consisting of two to four small circuli near the center of the scale. In some cases this first annulus could be seen only in one or two scales while it was missing in the other scales from the same fish; in others the first annulus was obviously missing, and in some cases doubtful. He therefore chose to add 1 yr to the age of all trout with five or more wide circuli between the first annulus and the center of the scale. Power (1969) had similar problems in age determination of Atlantic salmon from rivers flowing north into Ungava Bay in northern Canada. He too chose to add 1 yr to the age of all salmon with five or more circuli before the first annulus.

These investigations show that the first annulus in scales of salmon and trout from cold waters consists of a few narrow circuli close to the center of the scale, or is missing. However, the temperature intervals where the problem exists have not been clearly defined, nor has the fraction of fish that do not acquire a first annulus been related to the temperature regime. This paper reports such data for salmon and trout from two rivers in northern Norway.

Description of the Rivers

The Beiarelva and Saltdalselva rivers are situated in the county of Nordland, northern Norway (67°N). The rivers have a drainage area of 1050 and 1550 km^2, respectively. Except

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TABLE 1. Mean and range of temperatures (°C) in the Beiarelva and Saltdalselva rivers in July and August 1976–79. The temperature was measured at 07:30 and 17:30 each 2nd day by the Norwegian Water Resources and Electricity Board — hydrology department.

		Beiarelva				Saltdalselva			
		1976	1977	1978	1979	1976	1977	1978	1979
July	Min	4.0	4.2	9.1	5.4	6.1	6.1	9.7	8.4
	Mean	6.7	6.4	11.1	8.4	9.4	9.1	13.4	11.4
	Max	9.2	9.2	13.2	11.7	12.4	11.6	16.8	15.0
Aug.	Min	4.2	7.8	6.8	6.5	7.4	7.6	8.8	8.6
	Mean	7.9	9.5	9.0	9.4	10.6	9.9	11.6	11.4
	Max	11.1	10.9	11.4	11.3	15.0	13.1	15.0	15.5

for the Vefsna River they are the largest salmon rivers in the county of Nordland, each with a total catch of salmon, anadromous brown trout, and anadromous Arctic char (*Salvelinus alpinus*) of 5–8 t/yr.

The drainage areas consist mainly of high mountains, birch forests, and in the lower regions some farm land. Some of the largest tributaries of the Beiarelva River drain the glacier Svartisen, giving Beiarelva a greygreen color in summer. This makes Beiarelva the coldest of the two rivers (Table 1) and probably one of the coldest salmon rivers in the world.

Materials and Methods

The material was collected with an electrical fishing apparatus between May 3 and May 10, 1977, 1978, 1979, and 1980, and preserved in formaldehyde for laboratory study.

The total length of the fish was measured by spreading the tail into a natural position.

Scale samples were taken in an area near the lateral line between the adipose and the dorsal fin (Dannevig and Høst 1931). Age determination and circuli counting were done using a binocular microscope with the scales in water. Otoliths were analyzed in doubtful cases and the maximum number of circuli on the scales of each fish was recorded. The basal plate was not included, and maximum numbers of circuli were found on scales in the row close to the lateral line. A total of 447 1-yr-old fish were investigated.

In early May fry had not yet emerged, and hence fry and 1+ fish could not be confused.

Results

ATLANTIC SALMON

Usually the smallest individuals had not yet formed scales (Fig. 1). The scales of the salmon in Beiarelva first appeared when the fish were 33–34 mm. Salmon specimens from Saltdalselva of critical lengths were scarce, but all individuals from this river with lengths of 36 mm or more had formed scales, while those 34 mm or shorter lacked them (Fig. 1).

The proportion of yearlings without scales varied from year to year in both rivers. During the cold summers of 1976 and 1977, fewer individuals reached the critical length than during the warmer summers of 1978 and 1979. In Saltdalselva a larger fraction of the yearlings had formed scales than in Beiarelva. In Beiarelva, the proportion of salmon without scales found in 1977, 1978, 1979, and 1980 was 77, 61, 15 and 10%, respectively. Data for Saltdalselva 1979 are lacking, but the corresponding results the other years were 13, 27 and 10%. On scales of salmon from Beiarelva two or three circuli were most frequently found (Fig. 2A). However, a considerable proportion of the yearlings had not yet formed scales. Five circuli were the highest found, and these in only 2% of the fish.

In scales of salmon from Saltdalselva, two to four circuli were most common (Fig. 2B). A larger fraction of the year-

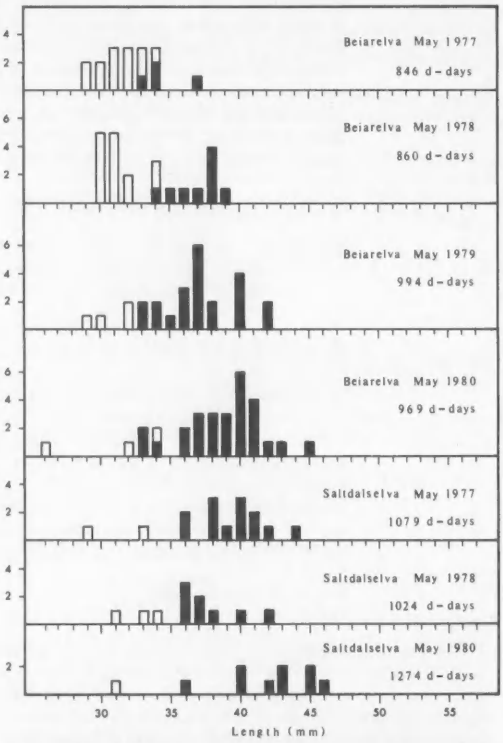

FIG. 1. Length–frequency of Atlantic salmon yearlings caught in the Beiarelva and Saltdalselva rivers in early May. White bars indicate fish without scales and black bars indicate fish with scales. The degree-days from May to October last year are given.

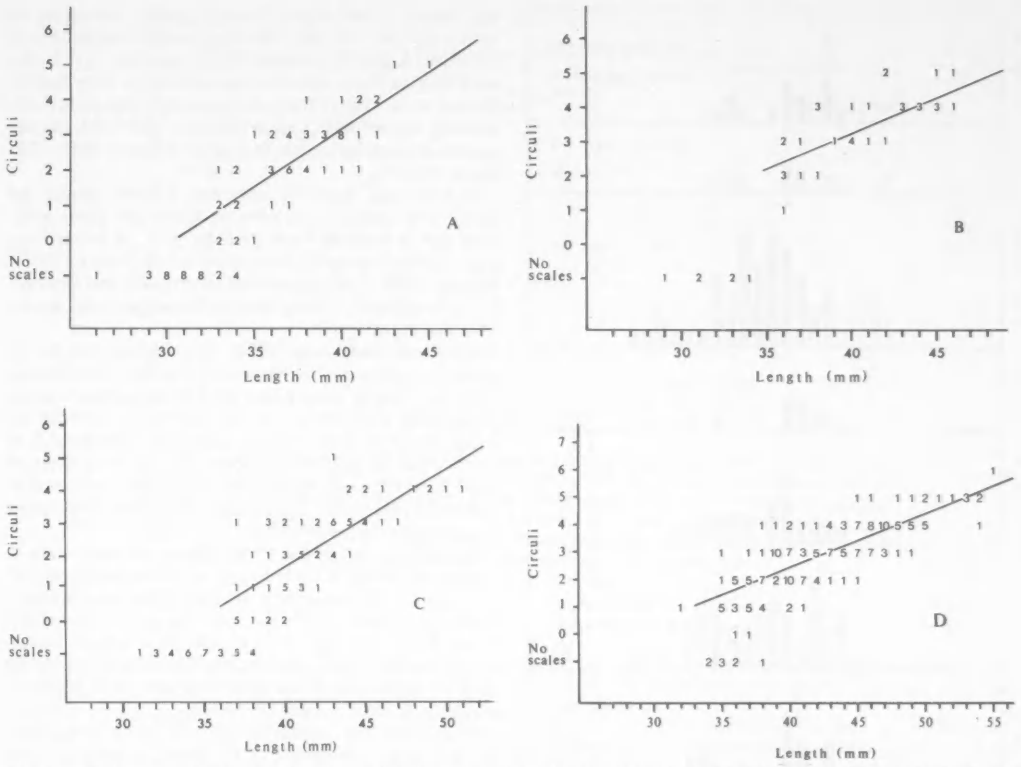

FIG. 2. Maximum number of circuli found on scales of yearling fish caught in early May 1977–80: (A) Atlantic salmon, Beiarelva River, (B) Atlantic salmon, Saltdalselva River, (C) brown trout, Beiarelva River, (D) brown trout, Saltdalselva River.

lings had formed scales here than in Beiarelva, but scales with five circuli were rather rare in this river too (7%).

BROWN TROUT

Similar results were found for brown trout as for Atlantic salmon, but the critical length for scale formation seemed to be somewhat larger. In Beiarelva the scales made their appearance when the lengths of the trout were 36–38 mm, while the trout in Saltdalselva formed their first scales at lengths of 35–38 mm, except one 32-mm-long individual (Fig. 3).

Only two trout were caught in Beiarelva in May 1977, both without scales. The proportion of trout without scales the following years were 48, 36, and 20% respectively. The percentage of trout without scales the 4 yr in Saltdalselva was 33, 4, 4, and 1%.

On scales of trout from Beiarelva, two or three circuli were most frequently found (Fig. 2C). Only 1% had scales with a maximum of five circuli.

In Saltdalselva, two to four circuli were most common (Fig. 2D). Five circuli were found on scales of about 7% of the trout, while six circuli were found on the scales of one trout.

Discussion

Paget (1920) discovered that the scales of trout (*Salmo fario*) reared under identical conditions make their appearance upon the body according to size, not age. Several papers report the size of fishes when the scales appear. The minimum length an Arctic char must attain before scales can be formed is 57–60 mm (Nordeng 1961). Cooper (1951) found the first scales of brook trout (*Salvelinus fontinalis*) to appear when the fish was 35–42 mm.

In brown trout, Parrott (1934) found that scales first appear at an average length of ~ 35 mm. Gunnerød (1966) found that scale formation occurred between 37 and 40 mm, while Jonsson (1976) found no scales in individuals smaller than 40–41 mm. Our results, 36–38 mm in Beiarelva and 35–38 mm in Saltdalselva, conform with these findings.

No papers dealing with the length of Atlantic salmon when the scales first appear have been available.

In cold rivers like Beiarelva and Saltdalselva, temperature seems to be an important factor influencing growth. Both bottom fauna and fish densities have been investigated. The same insect groups predominated in both rivers, and the densities of animals were about 80% higher in Beiarelva than in Saltdalselva (Koksvik 1977, 1978). The densities of salmon

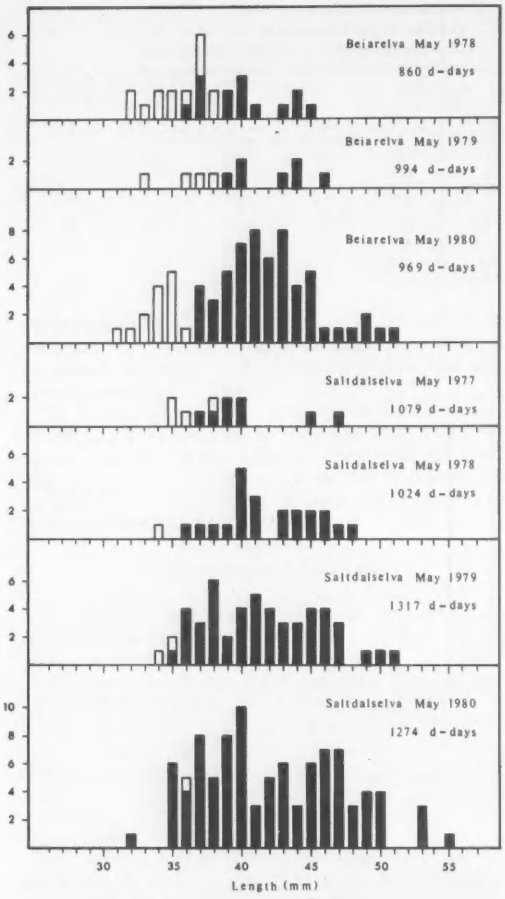

FIG. 3. Length–frequency of brown trout yearlings caught in the Beiarelva and Saltdalselva rivers in early May. Symbols as in Fig. 1.

and trout have been sampled with an electrical fishing apparatus for 6 yr in both rivers; the highest numbers were found in Saltdalselva (unpublished data). In spite of lower densities of food animals and higher densities of fish, the length of both salmon and trout were always greatest in Saltdalselva. The extremely low temperatures in Beiarelva are probably the main reason for this.

The degree-days from May to October were used as a measure of the temperature conditions in the rivers each year. This was correlated with the formation of scales of salmon and trout (Fig. 4). An exponential function has been fitted to the data by the method of least squares. A considerable fraction of the fish lacked the first annulus when the degree-days from May to October were less than 1000–1100 (Fig. 4); errors in age determination because of lack of the first annulus were minor when fish were exposed to >1100 degree-days.

In Canada, the most northerly known populations of Atlantic salmon are found in rivers flowing north into Ungava Bay. Power (1969) reported annual growth increments of salmon parr of ~ 30 mm, which is somewhat higher than in Beiarelva. A generalized mean daily temperature curve for the main Ungava rivers indicates the degree-days from May to October to be 1200–1300 in normal years. This means considerably warmer water than in Beiarelva (850–1000 degree-days) and somewhat warmer than in Saltdalselva (1000–1300 degree-days).

In Greenland, naturally spawning Atlantic salmon are known with certainty only from the Kapisigdlit River at the inner part of Godthåp Fjord (Nielsen 1961). A temperature curve for the Kapisigdlit River, reported by Nielsen (1961), indicates 1600–1700 degree-days between May and October. This is considerably warmer than the Norwegian rivers reported in this paper.

In Iceland, Gudjonsson (1978) expected that when the fry grow slowly through their first summer in the colder salmon rivers, and also in warmer ones after a cold spring or during an unusually cold summer, an annulus will not form in the scales during their first year in the river. Therefore, it is possible that an unknown number of smolts from rivers in western, northern, and northeastern Iceland are 1 yr older than indicated by the scales. Temperature curves from these rivers are unfortunately not available.

On the East coast of the Atlantic Ocean all rivers south of Norway are probably warm enough to ensure the presence of a first annulus. However, in some rivers in northern Norway, the Arctic region of USSR, and some glacial rivers in western Norway, the water temperature probably is so low during normal summers that a considerable proportion of the fry do not form scales. Our results should indicate where problems are likely to occur in other cold rivers.

Allen (1940, 1941) considered that 7°C was a critical temperature in the life history of the young Atlantic salmon. Below 7°C the fish appear to be lying quiescent in sheltered places, feeding very little, and not growing. This was tested using salmon data from Beiarelva and Saltdalselva in seeking better temperature criteria relating to scale formation in this species; calculations have shown a considerably better correlation to the number of days with a water temperature above 6.5°C (Fig. 5) than for 7.0°C ($r = 0.874$) or 6.0°C ($r = 0.979$). In years when the water temperature exceeded 6.5°C for more than 70–80 d per year, only minor errors arose in age determination of the salmon; less than 70–80 d per year, a correction was necessary for the individuals which lacked the first annulus in their scales.

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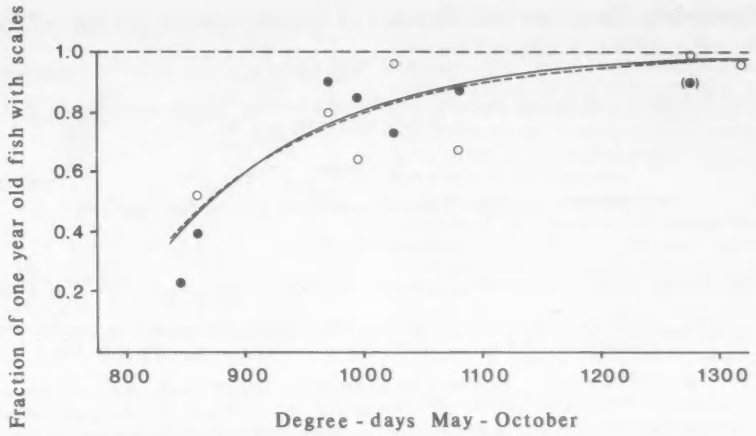

FIG. 4. Correlations between the water temperature and the fraction of 1-yr-old fish with scales which were caught in early May in the Beiarelva and Saltdalselva rivers. The degree-days from May to October are used to indicate the water temperature each year. The regression curves are for Atlantic salmon (black circles, unbroken line) $y = 1 - 322 \cdot e^{-0.0074x}$ ($r = 0.809$), and for brown trout (white circles, broken line) $y = 1 - 201 \cdot e^{-0.0069x}$ ($r = 0.756$). The data for salmon from May 1980 were excluded from these calculations because the sample was small and unrepresentative (point in parenthesis).

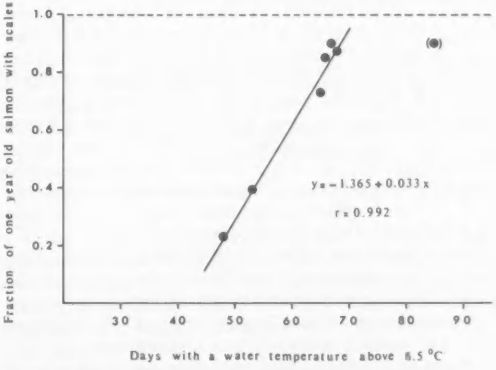

FIG. 5. Correlation between the number of days per year with a water temperature above 6.5°C in the Beiarelva and Saltdalselva rivers and the fraction of yearling Atlantic salmon with scales. We excluded the same sample as in Fig. 4.

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Community Structure and Biomass of Euphausiids in the Bay of Fundy

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KULKA, D. W., S. COREY, AND T. D. ILES. 1982. Community structure and biomass of euphausiids in the Bay of Fundy. Can. J. Fish. Aquat. Sci. 39: 326–334.

Seven species of euphausiids were found in the Bay of Fundy: *Meganyctiphanes norvegica*, *Thysanoessa inermis*, *T. longicaudata*, *T. raschii*, *T. gregaria*, *Euphausia krohnii*, and *Nematoscelis megalops* (listed in descending order of abundance). A high-intensity sampling scheme during November and March facilitated detailed distributional studies which revealed that *M. norvegica*, *T. inermis*, and *T. longicaudata* each had a specific stationary center of abundance in the study area, and each species performed a different pattern of diurnal vertical migration. *Meganyctiphanes norvegica* formed 90% (constituting 70 kt) of the euphausiids. The last four species were occasional immigrants from areas south of the Bay of Fundy. From the relationships between life history stages, vertical migration patterns, distribution, and currents in the Fundy Region, we suggest that these euphausiid species form stocks.

Key words: euphausiids, *Meganyctiphanes norvegica*, *Thysanoessa inermis*, *Thysanoessa longicaudata*, biomass, community structure, stock, Bay of Fundy

KULKA, D. W., S. COREY, AND T. D. ILES. 1982. Community structure and biomass of euphausiids in the Bay of Fundy. Can. J. Fish. Aquat. Sci. 39: 326–334.

On a trouvé dans la baie de Fundy sept espèces d'euphausides : *Meganyctiphanes norvegica*, *Thysanoessa inermis*, *T. longicaudata*, *T. raschii*, *T. gregaria*, *Euphausia krohnii* et *Nematocelis megalops* (par ordre d'abondance décroissant). Grâce à un programme d'échantillonnage intense en novembre et mars, on a pu mener des études détaillées de la distribution. C'est ainsi qu'on a constaté que *M. norvegica*, *T. inermis* et *T. longicaudata* ont chacun un centre d'abondance stationnaire spécifique dans la région étudiée et que chaque espèce a une migration verticale nycthémérale de caractère spécifique. *Meganyctiphanes norvegica* constitue 90 % (70 kt) des euphausides. Les quatre dernières espèces sont des immigrants occasionnels des régions du sud de la baie de Fundy. En nous basant sur les relations entre les stades du cycle biologique, les caractéristiques de la migration verticale, la distribution et les courants dans la région de Fundy, nous croyons que ces espèces d'euphausides forment des stocks.

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EUPHAUSIIDS occur in vast numbers in all oceans and along with copepods, make up most of marine zooplankton. Consequently they are a very important link in marine food webs at the intermediate level. Their large size and habit of forming concentrations, such as the sound-scattering layer (Sameoto 1976), makes them particularly accessible to a wide variety of predators. Most of the larger marine predators including commercial species at some stage feed directly or indirectly on euphausiids (Mauchline and Fisher 1969). This holds true in the Bay of Fundy and is illustrated in feeding studies by Battle et al. (1936), Tyler (1972), Barker (1976), Braune and Gaskin (1981), and others.

In spite of the importance of euphausiids in the trophic scheme, there exists a paucity of detailed population and community structure work, creating a rather significant gap in our knowledge of marine ecosystems. A bibliographic review of all euphausiid studies done in Canadian waters is given by Shih et al. (1971). This synopsis shows that before 1970 only Fish and Johnson (1937) and Lacroix (1961, 1968) go beyond

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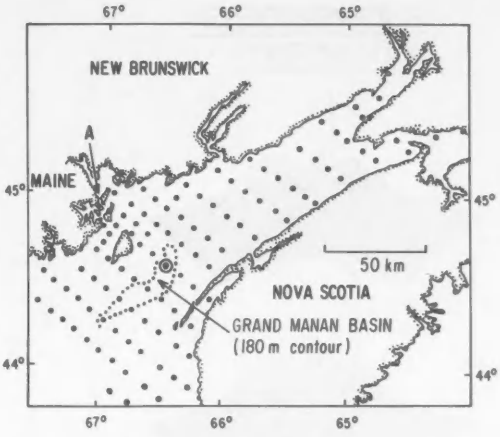

FIG. 1. Chart of the Bay of Fundy region showing the 180-m bottom contour line, location of the deep Grand Manan Basin, and the grid of stations for the horizontal distribution study. A, location of life history study, ○, location of vertical distribution study.

geographic records or general distribution studies. More recently, Lacroix and Bourget (1973), Berkes (1976, 1977a) in the Gulf of St. Lawrence, and Hollingshead and Corey (1974) and Kulka and Corey (1978) in the Bay of Fundy go one step further by dealing with more detailed aspects of life history and ecology. However, only Berkes (1977b) and Lindley (1980) approach the subject of production and biomass. Although there is a wealth of information on life history of euphausiids in other areas of the world, few authors have addressed the question of community structure in a detailed manner.

In the present study an unprecedented high-intensity sampling scheme carried out in a physically and hydrographically semienclosed area provided a unique opportunity to produce accurate estimates of biomass and allow a detailed view of population structures and interrelationships of the various species encountered. The resulting patterns observed led us to question the view expressed by many students of planktology that macroplanktonic ecosystems are relatively unstructured.

Materials and Methods

Samples were obtained from 116 stations 8−13 km apart covering the Bay of Fundy (area 1.48×10^4 km^2, Fig. 1): from November 16 to 29, 1972, February 28 to March 13, 1973, November 20 to 27, 1973, March 6 to 12, 1974, and November 5 to 13, 1974, yielding a very high sampling density. This series was supplemented by a number of nonquantitative samples taken in August 1975 near the center of concentration. The study area included all of the Grand Manan Basin. The above surveys were part of an extensive herring larval program carried out from 1969 to date, and detailed sampling methods are described in Iles (1971) and Stobo and Iles (1973).

The entire water column was sampled by towing obliquely, high-speed 61-cm Bongo nets (505 μm) equipped with a flowmeter. The gear was brought as near the bottom as possible ensuring complete sampling of the water column both day and night. Weights and numbers of each species of euphausiid in the samples were quantified, and the resulting figures were converted to wet weights and numbers below each square metre of surface using unpublished data on preserved to wet weight relationships. Biomass was then determined using areal expansion.

The lengths of tows were about 1.5−3 km long and the stations were 8−13 km apart. The sample design allowed for a reasonable integration of small-scale variability around the station and therefore produced a representative mean for that set making an estimate of biomass for the area possible. Numbers and biomass per square metre and relative percentages of each species of euphausiid in the Bay of Fundy were calculated for the five time intervals sampled.

The distribution of relative biomass for the three dominant species, *Meganyctiphanes norvegica*, *Thysanoessa inermis*, and *T. longicaudata* and total euphausiids were plotted using the Calcomp computer printer yielding three-dimensional "mountain peak" distribution diagrams. Because of the great differences in relative biomass between species, plots were made using a different scale for each species and month so that maximum peak size was the same for all plots regardless of abundance. The numbers of the less-common species (*T. raschii*, *T. gregaria*, *Nematoscelis megalops*, and *Euphausia krohnii*) along with larval stages were small and therefore a nonquantitative distribution (record of presence) was plotted for each.

Stations from all time periods sampled were classified according to the depth of water column and then grouped into a series of 10-m-depth categories. The mean number/m^2 of *T. inermis* and *M. norvegica* for each group was calculated so as to relate abundance to water column depth.

A preliminary vertical distribution study was carried out from the Bay of Fundy (44°34′30″N, 66°27′00″W) (Fig. 1) in November 1975. Four series of tows using 505-μm Bongo nets were done at 24:00, 06:00, 12:00, and 17:00. At each time interval seven or eight tows were made as follows: 10−20 m, 36−46 m, 61−71 m, 83−93 m, 102−112 m, 123−133 m, 143−153 m, and 173−183 m. The gear was lowered to the deepest level of each sample depth range as quickly as possible with most of the movement during this time straight down rather than horizontal in order to minimize the number of animals caught above the test depth. Conversely, the net was returned to the surface rapidly with most of the motion vertical. Length of tow at test depth greatly exceeded shooting and hauling time and was also long enough to integrate small-scale patchiness. Time sequences in and out of test depth range were recorded.The weights and numbers of euphausiids were quantified. Because the nets were open when towed to the surface through the water layer above each test depth, it was necessary to adjust for the error caused by animals caught above, even though the error was small. It was possible, using a compound correction factor derived from data collected in each test depth above, to find the proportion of each sample which was caught within the test depth range. The number of euphausiids from a given tow was corrected by dividing total time of that tow spent shooting and hauling by the total time of the previous tow. The result was then multiplied by the total number of animals caught in the previous

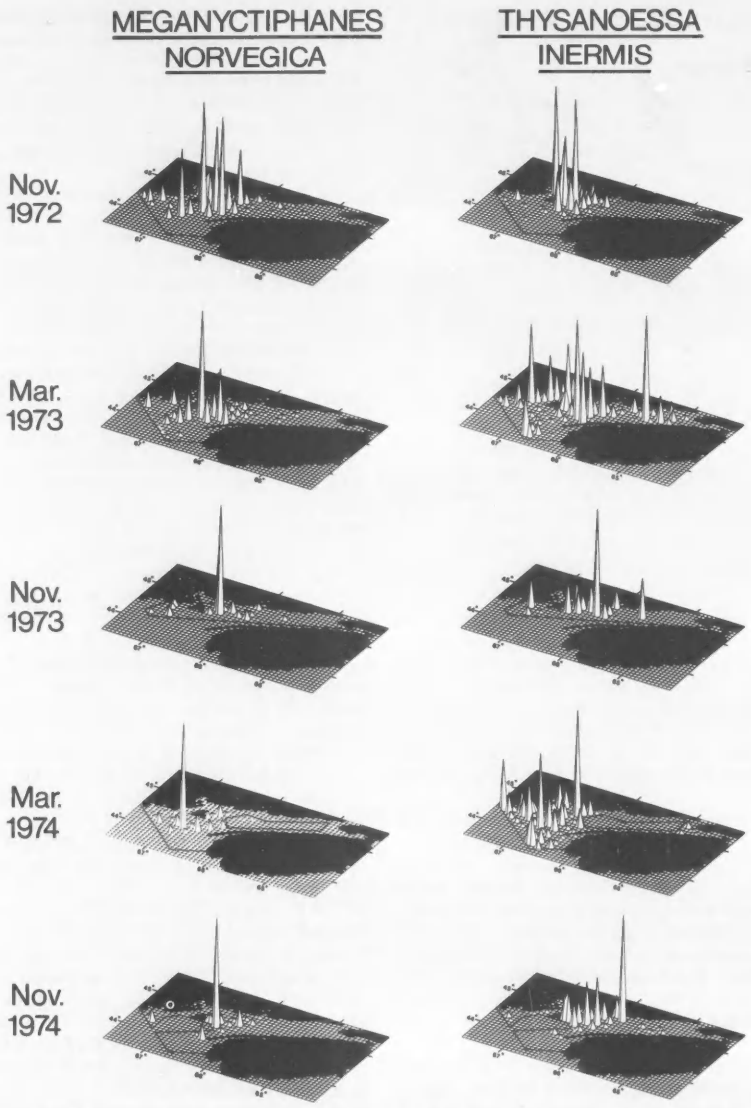

FIG. 2. Distribution of euphausiids in the Bay of Fundy. The dotted line represents the boundary of the area sampled. In each graph the maximum ordinate height has been standardized to a norm, but in each case represents a different percentage of the total species population. Total peak heights in each figure comprise 100% of that species at that time.

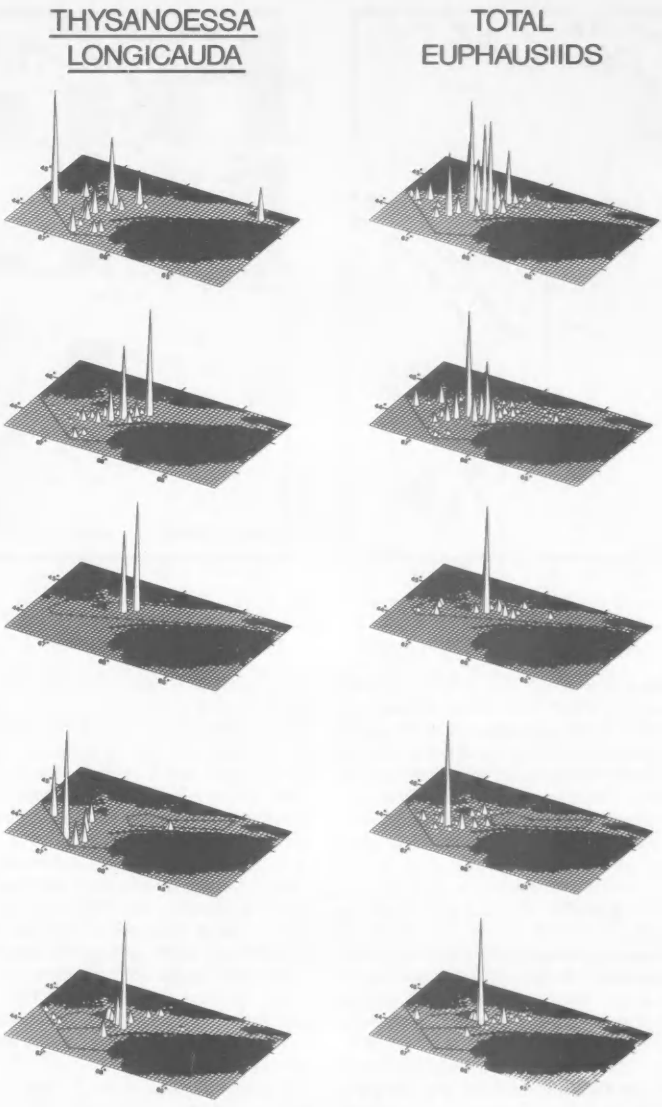

FIG. 2. (*Continued*)

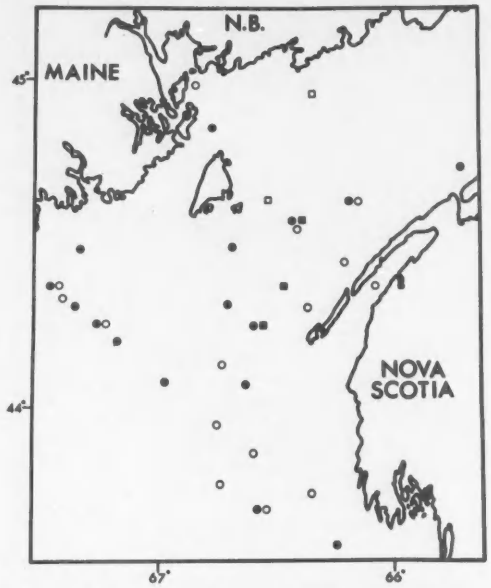

FIG. 3. Bay of Fundy showing stations where the uncommon species of euphausiids were caught. ●, *Thysanoessa raschii*; ○, *Thysanoessa gregaria*; □, *Euphausia krohnii*; ■, *Nematocelis megalops*.

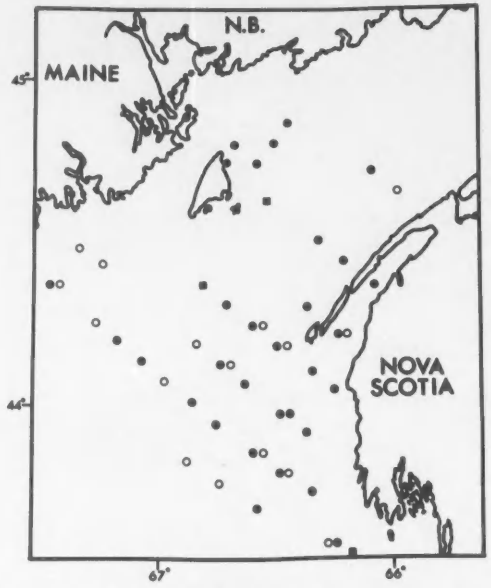

FIG. 4. Bay of Fundy showing stations where euphausiid larvae were caught. ○, November 1972; ■, November 1973; ●, November 1974.

tow (tow series from shallow to deep). This product, plus the products derived from any other tows above current test depth, were subtracted from the number of animals in the sample being corrected, giving the numbers in that test depth range corrected for animals caught during ascent and descent of the gear. This method eliminated the bias caused by animals taken out of test depth assuming that numbers per unit volume in the test depth range is representative of numbers between that range and the one above.

Results

The following seven species of euphausiids were recorded: *T. inermis*, *T. longicaudata*, *T. gregaria*, *M. norvegica*, *E. krohnii*, and *N. megalops*. The three predominant species in order of relative abundance were *M. norvegica*, *T. inermis*, and *T. longicaudata* (Fig. 2).

During November and March the distribution of *M. norvegica* showed little difference and was localized in the Bay of Fundy area, with the center of concentration over the Grand Manan Basin at 44°20′N, 66°30′W. Also, a series of short tows done in August 1975 in the area of highest predicted concentration yielded numbers per square metre similar to that seen in November and March samples. *Meganyctiphanes norvegica* did not extend into the Passamaquoddy area, the inner Bay of Fundy, or onto the southwest Nova Scotia shelf in large numbers. The distribution of *T. inermis* was also localized with a center slightly to the north of *M. norvegica*. In March 1973 *T. inermis* showed greater dispersion north and east into the inner Bay of Fundy. At all times there was considerable overlap in the distribution of *T. inermis* and *M. norvegica* and there was also some indication of other concentrations of both species in the extreme southwestern corner of the study area (Fig. 2).

The distribution of *T. longicaudata* was not as persistent as *M. norvegica* and *T. inermis*, and it tended to be more dispersed with no distinct center of concentration within the area sampled. It appeared in the Bay of Fundy in significant concentration only in March 1973.

Thysanoessa raschii constituted only a very small portion of the euphausiids in the area, but was found regularly in the southern part (Fig. 3). *Thysanoessa gregaria*, *N. megalops*, and *E. krohnii* were new records for the Bay of Fundy and occurred only rarely in both November and March in a scattered pattern in the deep, southern basin (Fig. 3).

In November 1972, 1973, and 1974, the larvae (all in late stages at this time of year) were concentrated in the southeast corner of the Bay of Fundy on the shelf off southern Nova Scotia (Fig. 4).

Meganyctiphanes norvegica made up 86–97% of the biomass of the euphausiids and 62–94% by number. *Thysanoessa inermis* made up most of the rest of the euphausiid biomass. In March 1973 there was an influx of *T. longicaudata* into the sample area so that it constituted 8% of the total community by number and 2% by weight, while in all other months sampled it made up less than 2% by number. Of about 75 000 animals examined, only 130 *T. raschii* (0.17% of total), 32 *T. gregaria* (0.04%), 7 *E. krohnii* (0.01%), and 2 *N. megalops* (0.003%) were found. The total estimated biomass of all euphausiids varied between 60 and 80 kt wet weight over the time period sampled (Fig. 5). *Meganyctiphanes norvegica* dominated with a biomass

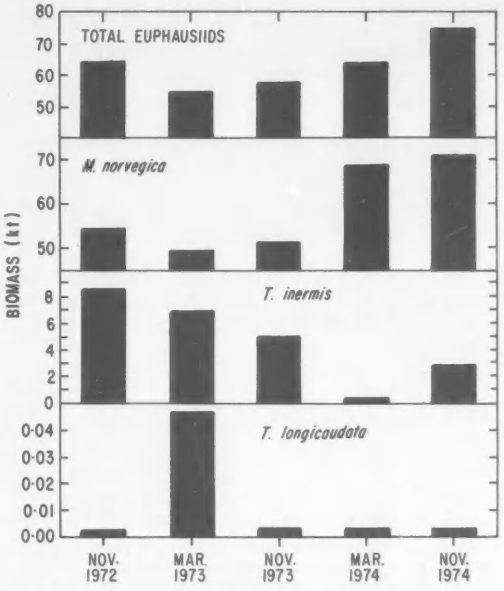

FIG. 5. Biomass of the euphausiids in the Bay of Fundy over a 2-yr period, November 1972 to November 1974.

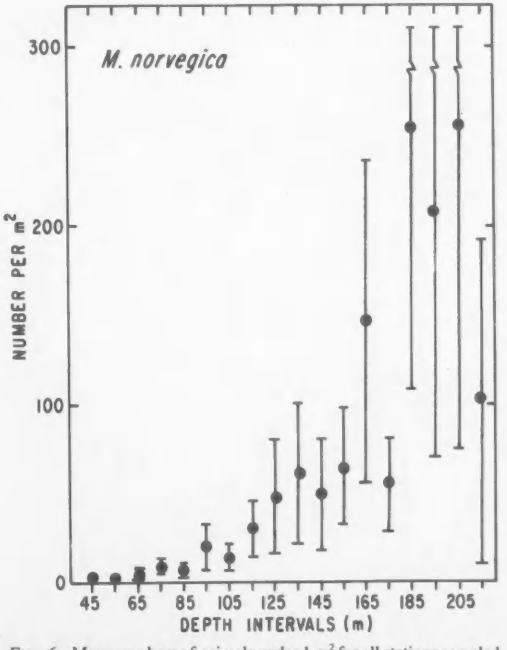

FIG. 6. Mean numbers of animals under 1 m^2 for all stations sampled in the Bay of Fundy in 10-m-depth intervals for *Meganyctiphanes norvegica*. Lines represent 95% confidence limits.

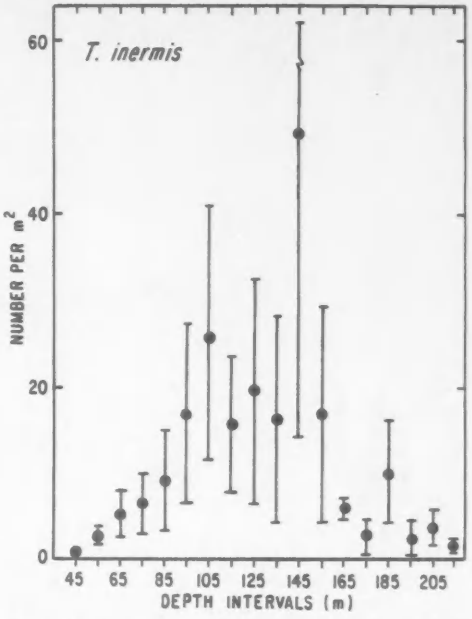

FIG. 7. Mean numbers of animals under 1 m^2 for all stations sampled in the Bay of Fundy in 10-m-depth intervals for *Thysanoessa inermis*. Lines represent 95% confidence limits.

ranging from 54 kt to 77 kt. The biomass of *T. inermis* gradually declined from 9.5 kt wet weight in 1972 to <1.1 kt by 1974 while *T. longicaudata* was <1 t for all months except March 1973 when it exceeded 5 t.

All populations fluctuated in biomass over the 2-yr period, but most remained concentrated in a small area over the Grand Manan Basin where bottom depth was 125–200 m. In this area of high concentration, euphausiid biomass reached 26.50 $g \cdot m^{-2}$ wet weight (250 m^{-2}) or 0.15 $g \cdot m^{-3}$, although the average for the whole area sampled was 5.5 $g \cdot m^{-2}$ or 0.045 $g \cdot m^{-3}$. *Thysanoessa inermis* was most abundant where bottom depth was 95–155 m and *M. norvegica* between 165 and 210 m. Neither species were found in waters with bottom depth <45 m (Fig. 6 and 7).

Diurnally, at 24:00 about 80% of *M. norvegica* were concentrated between 20 m and the surface, and no animals were found deeper than 70 m. At 06:00, the animals became more diffuse in the water column so that 70% of the animals were now within 70 m of the surface. By noon, all animals had descended below 70 m and by 17:00 they had again begun to ascend (Fig. 8). A ratio of total weight to total number of *M. norvegica* decreased gradually from the bottom (0.141) to the surface (0.103) at 24:00, from 0.180 to 0.144 at 06:00, and from 0.212 to 0.120 at 12:00, indicating that the larger and therefore the older animals were found at greater depths at all times.

Thysanoessa inermis exhibited a pattern similar to *M. norvegica*; however, the migration of *T. inermis* to the surface at night was not as pronounced (Fig. 8). Animals

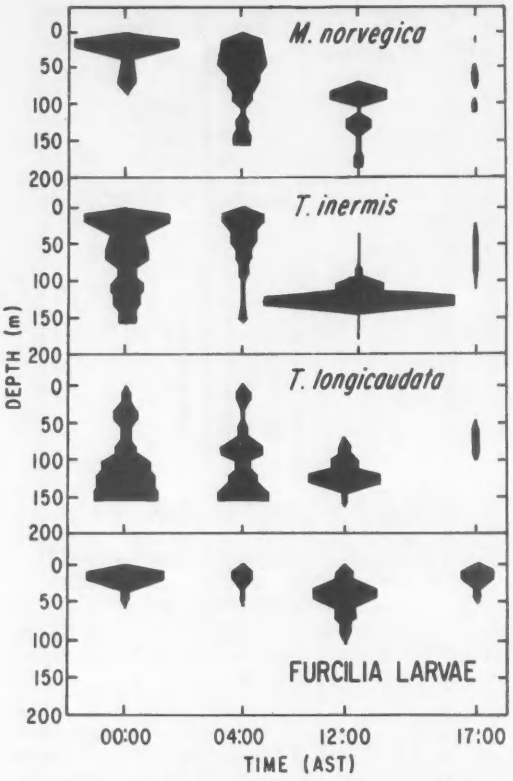

FIG. 8. The diurnal vertical migration patterns of *M. norvegica*, *T. inermis*, *T. longicaudata*, and larvae on November 10 and 11, 1975. The widths are proportional to the numbers caught at different depths and times for each species.

were found at all depths sampled, 33 and 40% were found within 20 m of the surface at 24:00 and 06:00, respectively. By 12:00 considerable downward migration had occurred with 80% of the animals located below 122 m, and none were found above 45 m. By 17:00 the animals had again begun to ascend.

Thysanoessa inermis were measured to determine population structure within the water column and it was found that 98% of the individuals were year-class 0 with an average carapace length between 3.42 and 3.97 mm at all depths (see Kulka and Corey 1978 for a description of life history stages). Less than 2% of the animals at all depths sampled were year-class 1. In all months sampled during the horizontal distribution study, substantial numbers of year-class 1 animals were taken in the oblique tows at the location where the vertical distribution study took place; therefore it is most probable that by not sampling the bottom 55 m during the vertical distribution study, most of year-class 1 was missed. Year-class 0 performed an extensive vertical migration at shallower depths separated from year-class 1 which stayed deep with little or no apparent vertical migration above 55 m off the bottom.

Thysanoessa longicaudata, a deeper-living species, showed only a limited migration to the surface at night (Fig. 8). At 24:00 75% were found below 105 m with only 2% in the top 20 m. This number increased slightly to 8% by 06:00, but 85% was still concentrated below 95 m. At 12:00 all animals had descended below 95 m with 63% of the population concentrated between 122 m and 133 m. The samples taken at 17:00 indicated that the animals were ascending at this time. A substantial part of the *T. longicaudata* population was probably missed by not sampling the bottom layers.

The larvae were all concentrated near the surface and 93–98% were found in the top 20 m at 24:00, 06:00, and 17:00. At 12:00 there was a small downward migration with a few animals reaching 90 m. However, 76% were found above 45 m. Weight-to-number ratios for the larvae examined at each depth showed that smaller larvae were found nearer the surface.

Discussion

The Bay of Fundy provides suitable conditions including appropriate temperature and depth ranges for *T. inermis* and *M. norvegica*. On the other hand *T. longicaudata* is an oceanic species generally found where depth exceeds 200 m (Jones 1969), and only a small portion of the Bay of Fundy provides such depths. *Thysanoessa raschii*, a more northern shelf species has the southern limit of its range in the Bay of Fundy. The other three species, *E. krohnii*, *N. megalops*, and *T. gregaria* are oceanic and are found in abundance in adjacent areas (personal observation) with only fringes of the population occurring in the sample area.

The distribution of *T. inermis* and *M. norvegica* overlap, but have different centers of concentration. This is probably partially due to different bottom-depth preferences for each species. *Thysanoessa inermis* preferred a bottom-depth range of about 100–150 m whereas *M. norvegica* stayed over the deeper part of the basin. Similar patterns were noted for both species on the Scotian Shelf (personal observation). No studies in the past have dealt specifically with the relationships of depth and concentration of euphausiids over specific areas, but worldwide distributions indicate that *T. inermis* and *M. norvegica* are found only in depths of about 100–400 m (Mauchline and Fisher 1969), consistent with this study.

The biomass of each species of euphausiid in the Bay of Fundy fluctuated independently from one another over the 2-yr study period. Such fluctuations reflect changes in oceanographic conditions, but throughout the study period species composition showed little change. *Meganyctiphanes norvegica* dominated with a biomass of about 70 kt being 90% by weight of the total euphausiids, and *T. inermis* made up the bulk of remaining biomass. The average relative biomass of total euphausiids in the Bay of Fundy was 0.04 $g \cdot m^{-3}$–0.05 $g \cdot m^{-3}$ and this compares with 0.012–0.045 $g \cdot m^{-3}$ recorded by Berkes (1977b) in the Gulf of St. Lawrence although species mix in the two areas was quite different.

Relatively consistent biomass levels were maintained in a small area of active mixing overlying the Grand Manan Basin. At the surface the main inflow of water into the Bay is on the

Nova Scotia side (Hachey and Bailey 1952). This current proceeds up the coast of Nova Scotia then northwest across the bay at the level of the St. John River flowing out along the New Brunswick coast into the Gulf of Maine. Bumpass and Lauzier (1965) found that a certain amount of surface flow crossed back onto the Nova Scotia side at the Grand Manan Island level setting up a weak surface anticyclonic system which may be used by the larval euphausiids as a transport retention mechanism during maturation. A similar mechanism was noted for euphausiids (Berkes 1976), fish larvae (Iles 1975), and calanoid copepods (Redfield 1941). The eggs are probably released into the surface layers over the Grand Manan Basin where the adult euphausiids are located. The larvae are concentrated near the surface in a separate set of currents than the adults and are probably carried away from them in this surface outflow along the New Brunswick side during the summer and fall. The eggs and early stages of larvae were found to be present in the Passamaquoddy Bay area in summer, but no larvae were found there beyond the mid-furcilia stages probably because they are being transported south of Grand Manan Island and across to the Nova Scotia side in this anticyclonic eddy. Late furcilia larvae were concentrated off southwest Nova Scotia, substantiating the possibility of such larval transport. The reduced vertical migration is such that the larvae remain within the surface eddy away from the adults and are not washed out of the Bay in the deeper currents. As they transform into adolescents they complete their horizontal migration, back in the area of adult concentrations.

Separate from the larvae, the adults of each species exhibited individual patterns of vertical distribution and migration extending throughout the water column. The pattern of *M. norvegica* was more extensive than *T. inermis* and the age structure of these two species was also ordered by depth. Year-class 0 and 1 *T. inermis* were segregated into separate layers, older animals nearer the bottom. Similarly, at the entrance to Passamaquoddy Bay for the same population, year-class 0 dominated the surface swarms (Kulka and Corey 1978), and older animals did not migrate out of the deep layers. Such patterns were also noted in the eastern Pacific and Barents Sea populations by Boldovskii (1937), Drobysheva (1957), Manteifel (1961), and Ponomareva (1963). Changes in morphology from year 0 to year 1, as described by Kulka and Corey (1978), accompanied this vertical niche change. Year-class 0 animals inhabited the midwater layers while year-class 1 appeared to be deep living. The configuration of year-class 0 *T. inermis* closely matched that described for predatory euphausiid species by Nemoto (1966, 1967) while the short appendages and smaller mandibules of year-class 1 individuals appeared better suited for a less carnivorous diet. The differences between the two year-classes are likely related to separate niche requirements. *Meganyctiphanes norvegica* also changes its vertical distribution with age, but there is no evidence of accompanying morphological changes with age. Both species are effectively partitioned by age-group and from each other to make better use of the resources available.

In general vertical distribution and migrations of each species are similar to patterns found in other areas. However, by comparing results of the present study to Mauchline (1960, 1966) in the Firth of Clyde, Matthews (1973) off Norway, and Berkes (1976) in the Gulf of St. Lawrence for *M. norvegica*; above-mentioned papers for *T. inermis*; Jorgensen and Matthews (1975) off Norway, and Berkes (1976) in the Gulf of St. Lawrence for *T. longicaudata*, it can be seen that populations from each area are distinctly different and exhibit seasonal variation. Because the Bay of Fundy is an area of energetic hydrographic conditions and the surface gyre does not extend into deeper layers (Lauzier 1967), it would not be possible for the adult euphausiid population to maintain themselves in stationary concentrations simply by swimming against the current nor would they be able to navigate a station in midwater using external cues. Hardy and Gunther (1935) suggested that vertically migrating animals would be displaced horizontally because of differential currents in the water column. A strategy then to concentrate and maintain position would be to migrate in a particular manner so as to "catch" an appropriate set of currents at the various depths through the day and night. Certainly a portion would be transported out of the area; however, enough would be retained to sustain the population. As noted above, the vertical migratory pattern of each population is different and is adapted to maintain position in separate local hydrographic conditions. Because it appears from this study that both the adults and larvae of Bay of Fundy euphausiids remain separated or partially separated from euphausiids in surrounding areas (i.e. Gulf of Maine and Scotian Shelf) they have possibly evolved into distinct stocks. This would be advantageous to the species allowing the animals to remain concentrated for efficient reproduction within a suitable area. Conversely if the populations were scattered and wandering, breeding would be sporadic, propagation would suffer, and adults would eventually find themselves in areas unsuitable for survival. Other zooplankton in the Bay of Fundy such as chaetognaths (Hurley, personal communication) and herring larvae (Iles 1975) also appear to concentrate and maintain a distinct center for all or a portion of their life cycle. Evidently it is not simply the effect of a large gyre concentrating the various species into one area because each one maintains its own distinct center away from the others. Most authors examining zooplankton in other areas have also noted uneven distribution and patchiness, therefore distinct population units or stocks maintained in position by a particular vertical migration strategy may be more general for macroplankton. This, however, remains quite speculative until there is evidence of genetic separation between various concentrations.

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Primary Production and Nutrient Assimilation by Natural Phytoplankton Populations of the Eastern Canadian Arctic

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HARRISON, W. G., T. PLATT, AND B. IRWIN. 1982. Primary production and nutrient assimilation by natural phytoplankton populations of the eastern Canadian Arctic. Can. J. Fish. Aquat. Sci. 39: 335 – 345.

Phytoplankton biomass (chlorophyll *a*) and primary production rates in Baffin Bay during summer 1978 were comparable to levels reported for other open water arctic and subarctic regions. Values were moderately high ($\bar{x}$ = 57 mg Chl·m^{-2}; 227 mg C-fixed·m^{-2}·d^{-1}) considering the low mixed-layer nutrient (nitrogen) concentrations, low ambient temperatures ($\bar{x}$ euphotic zone = −0.2°C), and variable and moderately low daily solar radiation ($\bar{x}$ = 6.9 MW·m^{-2}). Biomass maxima were consistently found at or near the bottom of the euphotic zone, and were 6 times higher than surface values on the average. Nitrate and ammonium were assimilated in approximately equal proportions despite the relatively greater abundance of nitrate in the euphotic zone, particularly below the mixed layer. Average C:N assimilation ratios were slightly lower (5:1) than the chemical composition ratio of the particulate matter (7:1). High phosphate assimilation rates reflected the abundance of this nutrient in the euphotic zone and resulted in low C:P (22:1) and N:P (6:1) assimilation ratios. Growth rates computed from carbon and nitrogen (NO_3^- + NH_4^+) assimilation rates averaged 0.31 and 0.35 doublings·d^{-1}, respectively, for the euphotic zone, and were half the maximum expected growth rates for prevailing water temperatures and optimal conditions of light and nutrients. Baffin Bay phytoplankton populations exhibited no obvious signs of severe nitrogen limitation despite low euphotic zone concentrations of the nutrient. Furthermore, the strong correspondence between: (1) normalized primary production rates (photosynthetic index) and incident solar radiation and (2) growth rates and incubation temperatures suggests that nutrients may play a relatively less important role in controlling arctic primary production than previously considered.

Key words: phytoplankton, primary production, nutrients, arctic, light, and temperature

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La biomasse phytoplanctonique (chlorophylle *a*) et les taux de production primaire dans la baie Baffin durant l'été 1978 était comparables aux niveaux signalés dans les autres régions de pleine eau arctiques et subarctiques. Les valeurs sont moyennement élevées ($\bar{x}$ = 57 mg Chl·m^{-2}; 227 mg C-fixé·m^{-2}·d^{-1}) compte tenu des faibles concentrations d'éléments nutritifs (azote) dans la couche mixte, les basses températures ambiantes ($\bar{x}$ dans la zone euphotique = −0,2°C) et la radiation solaire quotidienne variable et moyennement faible ($\bar{x}$ = 6,9 MW m^{-2}). Les maxima de biomasse ont toujours été observés au fond ou près du fond de la zone euphotique et étaient en moyenne de six fois supérieurs aux valeurs de surface. Les nitrates et l'ammoniac sont assimilés en proportions à peu près égales, en dépit de l'abondance relativement supérieure des nitrates dans la zone euphotique, particulièrement au-dessous de la couche mixte. Les rapports moyen d'assimilation C:N sont légèrement inférieurs (5:1) au rapport de la composition chimique de la matière particuliaire (7:1). Les taux élevés d'assimilation des phosphates reflètent l'abondance de ce nutriment dans la zone euphotique et sont la cause de faibles rapports d'assimilation C:P (22:1) et N:P (6:1). Calculés à partir des taux d'assimilation du carbone et de l'azote (NO_3^- + NH_4^+), les taux de croissance sont en moyenne de 0,31 et 0,35 doublement d^{-1} respectivement dans la zone euphotique et sont deux fois moindres que les taux de croissance maxima anticipés aux températures de l'eau prévalentes et aux conditions optimales de lumière et d'éléments

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nutritifs. Les populations phytoplanctoniques de la baie Baffin ne montrent pas de signes évidents de sérieuse limitation d'azote en dépit de faibles concentrations du nutriment dans la zone euphotique. En outre, l'étroite correspondance entre: 1) les taux de production primaire standardisés (indice photosynthétique) et la radiation solaire incidente, et 2) les taux de croissance et les températures d'incubation laisse supposer que les éléments nutritifs jouent un rôle relativement moins important qu'on le croyait dans le contrôle de la production primaire arctique.

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DISTRIBUTION and abundance of phytoplankton in polar and subpolar seas have been studied for several decades (Knox 1970; Allen 1971; Fogg 1977). Relatively few studies, however, have dealt with phytoplankton production dynamics and the influence of the unique high latitude environment on the photosynthetic process. El-Sayed (1970, 1978), Fogg (1977), and Nemoto and Harrison (1981) have reviewed much of this work.

Arctic and antarctic seas share two common physical characteristics important for phytoplankton growth: low seawater temperatures and extreme seasonal oscillations in solar radiation. They differ in dissolved nutrient chemistry and the seasonally changing areal extent of sea ice. In the Antarctic, sea-ice cover may vary by a factor of 10 between summer and winter whereas overall reduction in arctic sea ice in summer may be less than 20% of the winter maximum (Foster 1978). Antarctic surface waters are characterized by their abundance of inorganic nutrients throughout the year. This results from continuous upwelling, driven by the antarctic circumpolar current system. In contrast, relatively restricted circulation in north polar regions results in summer meltwater significantly diluting surface waters and commonly producing a shallow and stable mixed layer. As a consequence, this near-surface layer becomes depleted in dissolved inorganic nutrients during a significant fraction of the open-water, productive season (Dunbar 1968).

Most polar phytoplankton research has been done in the southern ocean. From this work, light has been identified as the most important factor limiting primary production (Holm-Hansen et al. 1977; El-Sayed 1978) although water-column stability (El-Sayed 1978; Fogg 1977) and more recently temperature (Slawyk 1979; Olsen 1980) have been considered important.

Arctic studies have been concentrated in the Pacific (Nemoto and Harrison 1981 and references cited therein), primarily in subarctic coastal waters (e.g. McRoy et al. 1972). Few studies of phytoplankton physiology have been done in arctic and subarctic Atlantic waters. From the biological and physical data available, Dunbar (1968, 1970) has suggested that the pronounced water-column stability and concomitant nutrient depletion in surface waters are the main factors controlling primary production in arctic seas.

In this paper we consider the extent to which this speculation is justified in light of observations we made of phytoplankton biomass and production rates on a cruise to the eastern Canadian Arctic (Baffin Bay) during the summer of 1978. Much of this work focused on the inorganic and organic nutrient chemistry of the water and suspended particulate matter, and the nutrient assimilative fluxes of the phytoplankton populations. Observations made in temperate latitudes (early phase of the cruise) are included for comparison.

Methods

SAMPLING

Fourteen stations were sampled during the first leg of CSS *Hudson* cruise 78-026 into Northern Baffin Bay from August 26 to September 21, 1978 (Fig. 1). On most days, water samples were collected at ~ 08:00 local time from five depths based on light penetration (corresponding to 100, 50, 25, 10, and 1% surface irradiance). Sampling depths were calculated by assuming logarithmic decrease in light with depth and three times secchi depth was equivalent to the 1% light level (here, defined as the euphotic zone). Water samples were collected using PVC plastic Nisken bottles (12- and 30-L capacity).

ANALYTICAL

Particulate matter was concentrated on glass fiber filters for analysis of chlorophyll *a* by the fluorometric method of Holm-Hansen et al. (1965) and particulate organic carbon and nitrogen by the dry combustion method described by Sharp (1974). Whatman® GF/C filters were used for chlorophyll, and precombusted Reeve-Angel® 984H glass filters for particulate organics. Filtrates were retained for nutrient (NO_3^-, PO_4^-, NH_4^+, $SI(OH)_4$) analysis by standard colorometric methods described by Strickland and Parsons (1972). Ammonium samples were analyzed immediately; the remaining nutrients were later determined from frozen water samples on a Technicon II auto-analyzer (Irwin et al. 1980). Salinity and temperature data were obtained from continuous profiles run prior to bottle sampling using a Guildline® CTD system. Incident solar radiation was measured at hourly intervals using a LICOR® LI-200S pyranometer sensor coupled to a recording integrator (LICOR LI550). Irradiance measured in langleys was converted to energy units using the relationships: $1\ ly \cdot h^{-1} = 41.9\ kW \cdot m^{-2}$.

TRACER EXPERIMENTS

Water samples from each depth were dispensed into transparent glass bottles for radioactive or stable isotope tracer experiments. To 250-mL samples ("time-zero," light and dark bottles), from 185 to 370 kBq of $NaH^{14}CO_3$ was added and the bottles incubated for 24 h in "simulated" in situ deck incubators corresponding to the light levels from which the samples were taken and cooled with near-surface seawater. After incubation, sample particulates were collected on glass fiber filters (Reeve-Angel 984H), rinsed with filtered seawater, and placed in scintillation cocktail (Aquasol) for analysis of radioactivity by scintillation spectrometry.

FIG. 1. Station locations for arctic cruise 78-026, August 26 to September 14, 1978.

Phosphorus-33 tracer experiments were done simultaneously using an experimental protocol similar to that of the ^{14}C samples. In this case, however, "dark" bottles were not done. The radioactivity level added was ~ 37 kBq per bottle.

Nitrogen-15 uptake was measured by adding $K^{15}NO_3$ (99 at % ^{15}N) and $(^{15}NH_4)_2SO_4$ (95 at % ^{15}N) in concentrations of 0.1 μg at·L^{-1} to 1000-mL samples and incubated along with the radiotracer samples. At the end of incubation, sample particulates were collected on glass fiber filters (Reeve-Angel 984H) and the filters frozen. In the laboratory, the sample filters were dried and prepared for ^{15}N analysis (micro-dumas combustion) by emission spectrometry (Fiedler and Proksch 1975). Nitrogen assimilation rates were computed according to the equations outlined by Dugdale and Goering (1967). Despite low initial nitrogen concentrations in the water samples from near the sea surface, nutrient exhaustion in the bottles was not a problem as consumption (after 24 h) averaged 20% of the initial concentration and exceeded 40% only in near-surface samples.

At the same stations, subsamples (125 mL) were also usually taken from two of the above depths (50, 1% light levels) for determination of the relationship between photosynthesis and light (light-saturation curve) by exposing carbon-14 labeled samples for 4 h to an artificial light gradient. Experimental procedures and a more detailed analysis of the results can be found in Platt et al. (1980).

Results

Distribution of Phytoplankton Biomass and Photosynthetic Production Rate

Although phytoplankton biomass and production rates ranged more than an order of magnitude within the euphotic zone (Table 1), a fairly consistent vertical structure was observed in both parameters for stations north of 60°N. Euphotic zone chlorophyll concentrations averaged 1.26 mg m^{-3}. Lowest values were found in surface waters and maximum values were typically found near the bottom of the mixed layer (Fig. 2). Although not shown in this figure, pycloclinal gradients at the bottom of the mixed layer were strong, typically 2.5 kg·m^{-3} in 5 m. Subsurface chlorophyll maxima were, on the average, 6 times greater than surface values (Table 1; Fig. 2, 3). Open-water stations often exhibited subsurface

TABLE 1. Mean values and ranges of arctic and subarctic phytoplankton biomass (chlorophyll *a* = Chl) and primary production rates (P.P.) for samples taken from the surface (*s*) and subsurface maxima (max). In each column, number of observations are on top, ranges in the middle, and means on the bottom. I_0 = total daily radiation.

Cruise	Date	Lat. (°N)	I_0 ($MW \cdot m^{-2}$)	Chl (*s*) ($mg \cdot m^{-3}$)	P.P. (*s*)[a] ($mg\ C \cdot m^{-3} \cdot d^{-1}$)	Chl (max) ($mg \cdot m^{-3}$)	P.P. (max) ($mg\ C \cdot m^{-3} \cdot d^{-1}$)	
77-024	Sept. 1977	60–78	17	17	17	17		Irwin et al. (1978d)
			2.0–10.8	0.08–4.90	2.1–20.8	0.28–6.86	—	
			5.7	0.68	5.6	1.98		
77-029	Oct. 1977	53–62	16	16	16			Irwin et al. (1978a)
			1.4–5.4	0.68–1.99	3.5–12.5	—	—	
			3.6	1.01	5.6			
78-002	Feb. 1978	50–59		16	16			Irwin et al. (1978b)
			—	0.09–0.27	0.5–4.1	—	—	
				0.17	1.9			
78-026	Sept. 1978	60–76	12	12	12	12	12	Present study
			3.4–12.6	0.19–1.40	4.7–22.8	0.94–8.30	5.7–25.1	
			6.9	0.57	9.5	3.55	13.2	

[a]For cruises 77-024, 77-029, and 78-002, daily primary production rates were estimated from hourly rates and day length using the equations derived by Platt (1971).

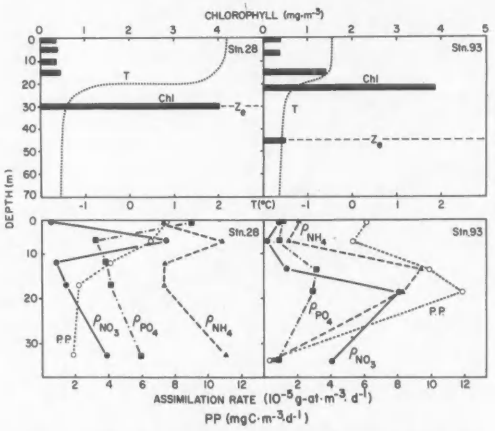

FIG. 2. Depth profiles of phytoplankton biomass (Chl) and production rates for representative nearshore (Stn. 28) and open-water (Stn. 93) stations.

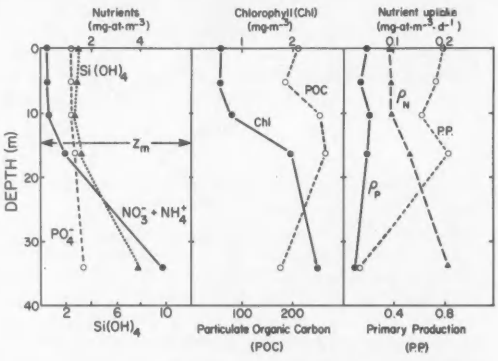

FIG. 3. Depth profiles of chemical and biological properties representing mean conditions for all Baffin Bay stations (Stn. 5–93). $\rho_N = (NO_3^- + NH_4^+)$ assimilation rate, $\rho_P = PO_4^-$ assimilation rate. Z_m = mixed layer depth.

maxima at the 10% light penetration depth ($\bar{x}$ = 16 m) while those more inshore had chlorophyll maxima at the bottom ($\bar{x}$ = 34 m) of the euphotic zone (Fig. 2). Although it cannot be clearly established from these stations that "true" maxima were located within the euphotic zone, as sampling did not exceed the 1% light depth, subsequent continuous fluorescence profiles to 100 m in the same general area and at the same time of year (A. Herman, Bedford Inst. Oceanogr., N.S., personal communication) have rarely shown chlorophyll maxima deeper than the euphotic zone.

A conspicuous latitudinal gradient was evident in primary production which covaried with temperature and solar radiation (Fig. 4, Table 2). In contrast, chlorophyll values were higher on the average for Baffin Bay stations than for the more southern stations.

Microscopic analysis of samples taken from the 50 and 1% light levels revealed that Baffin Bay stations were dominated by diatoms, which often accounted for over 90% of the numerical abundance. Representatives of the genera *Thalassiosira*, *Chaetoceros*, *Rhizosolenia*, and *Nitzchia* were most common (T. Platt unpublished data).

NUTRIENT CONCENTRATIONS AND ASSIMILATION RATES

Mixed layer nutrient concentrations for all Baffin Bay stations were consistently low for inorganic nitrogen (NO_3^-, NH_4^+) and high for PO_4^- and $Si(OH)_4$ (Fig. 3). Mean values were 0.15, 0.08, 1.19, and 2.87 mg-at·m^{-3} for NO_3^-, NH_4^+, PO_4^-, and $Si(OH)_4$, respectively. Concentrations of NO_3^- and $Si(OH)_4$ increased at the pycnocline while PO_4^- and NH_4^+ were relatively constant with depth. Total inorganic nitrogen ($NO_3^- + NH_4^+$) and $Si(OH)_4$ at the bottom of the euphotic zone averaged 4.72 and 7.91 mg at·m^{-3}, respectively. At nearly all Baffin Bay stations, PO_4^- and $Si(OH)_4$ concentrations in near-surface waters were noticeably higher in absolute terms and in relation to nitrogen concentrations,

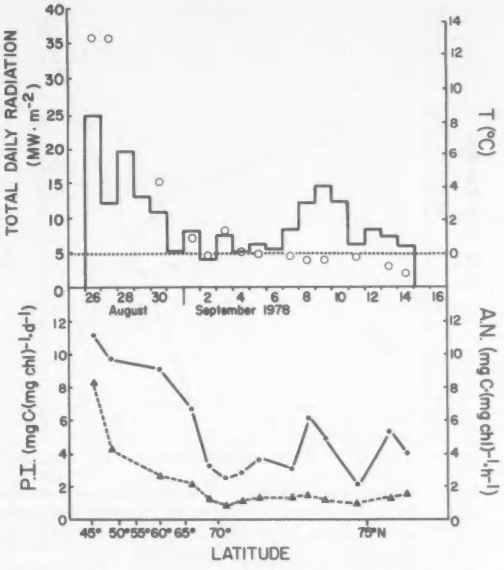

FIG. 4. Latitudinal variations in euphotic zone temperature (○), solar radiation (histogram), and primary production during arctic cruise 78-026. P.I. (●) computed from euphotic zone integral chlorophyll and in situ production rates (Table 2). A.N. (▲) from light-saturation experiments, 50% light penetration depth (Irwin et al. 1980).

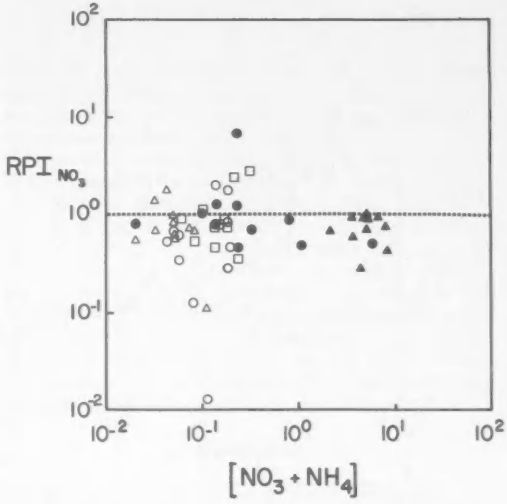

FIG. 5. Relationship between NO_3^- Relative Preference Index (RPI) and total inorganic nitrogen concentration (mg-at·m^{-3}) for Baffin Bay stations (Stn. 5–93). Light levels: 100%(○), 50%(△), 25%(□), 10%(●), 1%(▲).

$$RPI_{NO_3} = \frac{\rho NO_3/\rho(NO_3 + NH_4)}{NO_3 \text{ concn.}/(NO_3 + NH_4) \text{ concn.}}$$

than have been observed at lower latitudes (Irwin et al. 1978c). For example, mixed-layer $(NO_3^- + NH_4^+):PO_4^-$ and $(NO_3^- + NH_4^+):Si(OH)_4$ ratios averaged 0.2 and 0.1, respectively, for Baffin Bay stations as compared with 1.0 and 0.9 at 45°N (Stn. 1).

Nutrient assimilation rates (ρNO_3, ρNH_4, ρPO_4) generally covaried with phytoplankton biomass and nutrient concentrations (Fig. 2, 3). For more open-water stations, nutrient assimilation was generally maximal for all three forms at the 10% light level. Closer inshore, maxima were found near the bottom of the euphotic zone (Fig. 2). On the average, nitrogen assimilation increased with depth as photosynthetic rate decreased while phosphate assimilation was relatively con-

TABLE 2. Euphotic zone (depth = Z_e) integral phytoplankton biomass, primary production, and nutrient assimilation rates for arctic cruise 78-026.

Stn.	Lat.	Z_e (m)	Chl (mg·m^{-2})	Assimilation rates (mg-at·m^{-2}·d^{-1}) ρCO_2	ρNO_3	ρNH_4	ρPO_4	Assimilation ratios (atomic) C:N	C:P	N:P	f^a
1	44°57′	66	39.5	36.7	0.83	8.64	5.06	3.9	7.3	1.9	0.09
2	48°09′	36	27.4	22.3	0.22	4.28	1.41	5.0	15.8	3.2	0.05
5	60°52′	27	30.4	23.0	1.47	2.14	2.54	6.4	9.7	1.4	0.40
8	67°23′	54	31.2	17.7	1.13	1.25	0.99	7.4	17.9	2.4	0.47
13	69°34′	27	108.1	28.3	1.54	2.30	1.20	7.4	23.6	3.2	0.40
40	71°18′	30	96.1	30.3	5.86	1.20	1.17	4.3	25.9	6.0	0.83
32	71°35′	30	77.1	18.8	1.54	2.27	3.83	4.4	4.9	1.1	0.36
28	71°37′	30	41.5	8.7	0.86	2.69	1.48	2.5	5.9	2.4	0.24
59	71°48′	30	55.1	27.6	3.79	1.11	0.71	5.6	38.9	6.9	0.77
52	72°15′	33	42.6	10.8	4.52	1.50	0.59	1.8	18.3	10.2	0.75
70	72°45′	30	26.1	10.8	3.11	0.71	0.25	2.8	43.2	5.3	0.81
83	74°46′	36	63.0	11.1	2.82	3.20	0.78	1.8	14.2	7.7	0.46
93	74°59′	45	79.6	26.8	1.91	2.24	0.88	6.5	30.5	4.7	0.46
90	75°58′	36	29.4	13.3	1.16	1.51	0.45	5.0	29.6	5.9	0.43
$\bar{x}$(5-93)		34	56.7	18.9	2.48	1.88	1.24	4.7	21.8	5.6	0.53

$^a f = \rho NO_3/\rho(NO_3 + NH_4)$.

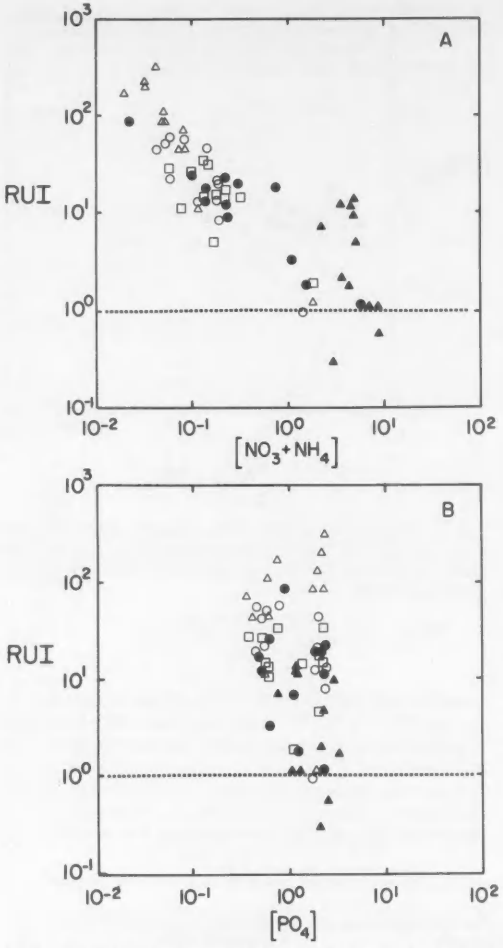

FIG. 6. Relationships between (A) relative utilization Index (RUI) and total nitrogen and (B) RUI and phosphate concentrations (mg-at·m^{-3}) for Baffin Bay stations (Stn. 5–93). RUI defined in text. Symbols as in Fig. 5.

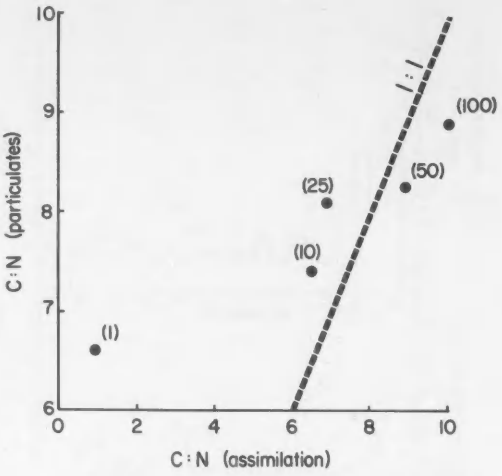

FIG. 7. Relationship between C:N atomic ratios of particulate matter, and assimilation rates. Mean values for Baffin Bay stations (Stn. 5–93). Numbers in parentheses represent light penetration depths and broken line signifies 1:1 relationship.

stant with depth (Fig. 3). Nitrate assimilation rates ranged from undetectable (usually in surface waters) to as high as 0.5 mg at·m^{-3}·d^{-1} at the bottom of the euphotic zone. Mean values were 0.038 mg at·m^{-3}·d^{-1} for the mixed layer and 0.066 for the entire euphotic zone. Ammonium assimilation rates were less variable and averaged 0.053 mg at·m^{-3}·d^{-1} in the mixed layer and 0.055 fo the euphotic zone. Phosphate assimilation rates ranged from 0.005 to 0.297 mg at·m^{-3}·d^{-1} with a euphotic zone average of 0.040 mg at·m^{-3}·d^{-1}. A clear latitudinal gradient in integral assimilation rates was not apparent although NO_3^- assimilation was somewhat higher at high latitudes and NH_4^+ and PO_4^- assimilation were generally lower (Table 2) Nitrate assimilation rates were noticeably higher in inshore stations compared to open water stations.

Nitrate and ammonium assimilation rates within the euphotic zone were similar (Table 2, last column). In the surface-mixed layer, NO_3^- averaged 40% of the total N (NO_3^- + NH_4^+) assimilation whereas in the chlorophyll-maximum layers, NO_3^- assimilation averaged 61% of the total; in the productivity maximum, the percentage was 43. When NO_3^-:NH_4^+ assimilation ratios were compared with the ratios of these nutrients dissolved in the water (Fig. 5), most samples showed a slight preference for NH_4^+ assimilation ($RPI_{NO_3} > 1 = NO_3^-$ preference, $<1 = NO_3^-$ rejection, or NH_4^+ preference (McCarthy et al. 1977). It is noteworthy that all samples from deep, nitrate-rich waters (depth of 1% surface irradiance) had values of RPI less than one.

Nitrogen (NO_3^- + NH_4^+) and PO_4^- assimilation ratios were also compared in a similar manner to the ratios of the corresponding dissolved nutrients. The Relative Utilization Index (RUI) is defined as:

$$\left[\frac{\rho(NO_3 + NH_4)}{\rho(PO_4)}\right] \div \left[\frac{(NO_3^- + NH_4^+) \text{ concentration}}{PO_4^- \text{ concentration}}\right]$$

where RUI > 1 means greater relative nitrogen utilization and <1 means greater relative use of phosphate. This might also be viewed as an index of potential nutrient limitation (i.e. an RUI >1 would suggest nitrogen exhaustion before phosphate). Practically all station depths showed RUIs greater than 1.0 with the highest values occurring in surface water where nitrogen concentrations were lowest (Fig. 6a). No relationship between RUI and PO_4^+ concentration was apparent (Fig. 6b).

Carbon:nitrogen, C:P, and N:P assimilation ratios were consistently low in Baffin Bay waters (Table 2). Assimilation ratios averaged 22 C:5.6 N:1 P compared to the Redfield ratios of 106 C:16 N:1 P (Redfield et al. 1963). Depth-related decrease in photosynthetic carbon assimilation and

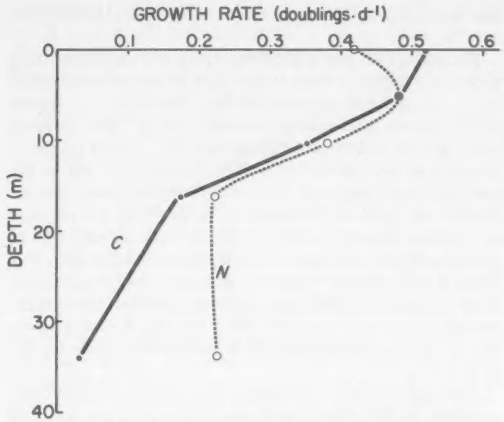

FIG. 8. Depth profile of phytoplankton growth rates computed for carbon (μ_C) and nitrogen (μ_N). Mean conditions for Baffin Bay stations (Stn. 5–93). Growth rate computations given in text.

increase in nitrogen assimilation (Fig. 3) resulted in an overall decrease in C:N assimilation ratios with depth. This pattern was also observed in the C:N composition ratio of the particulate matter (Fig. 7) although the magnitude of change of the latter was not as great. Assimilation ratios were comparable to particulate compositional ratios between the 25 and 50% light levels on the average.

GROWTH RATES

Specific growth rates (μ in doublings·d^{-1}) of phytoplankton were estimated using the relationship:

$$\mu = \log_2 \left[\frac{PC + \Delta PC}{PC}\right]$$

where PC = phytoplankton carbon; ΔPC = daily photosynthetic rate. Phytoplankton carbon was approximated from the slope of the particulate organic carbon and chlorophyll *a* regression using data from the chlorophyll maximum layers. From this analysis, the phytoplankton carbon was estimated to be 42 × chlorophyll *a* concentration (g/g). A similar analysis was done for particulate organic nitrogen (PON/Chl = 6.7), permitting nitrogen-specific growth rate calculations. Carbon-based growth rates varied from 0.01 to 0.76 doublings·d^{-1} ($\bar{x}$ = 0.31) for Baffin Bay stations. Nitrogen growth rates were slightly higher with a range of 0.08 to 1.03 doublings·d^{-1}, and a mean of 0.35. Growth rates decreased with depth, with carbon-specific rates highest at the surface, and nitrogen-specific rates highest at the 50% light level (Fig. 8). Overall, estimates of carbon and nitrogen growth rates were similar except at the 1% light penetration depth.

Discussion

ARCTIC PHYTOPLANKTON BIOMASS AND PRODUCTION

Phytoplankton biomass and production, averaged for the euphotic zone, were 1.26 mg Chl·m^{-3} (57 mg·m^{-2}), and 7.4 mg C·m^{-3}·d^{-1} (227 mg·m^{-2}·d^{-1}) in Baffin Bay during late summer 1978. Although most stations were relatively close inshore, values for open waters were not substantially different. In addition, late summer mean values from the previous year in the same general area and from adjacent eastern subarctic waters were comparable (Table 1).

Summer phytoplankton production levels in Baffin Bay were similar to open-water values in other arctic regions but

TABLE 3. Average phytoplankton biomass and primary production rates from selected arctic and subarctic waters in summer.

Location	Lat. (°N)	Chlorophyll (mg·m^{-2})	Primary production (mg C·m^{-2}·d^{-1})	Source
Atlantic				
E. Greenland (Coastal)	55–70	—	>350	Steeman-Nielsen (1958)
(Open water)		—	100–200	
Davis Strait	60	20	21	MacLaren-Marex, Inc. (1979)
E. Canadian Arctic	64	100	450[a]	Grainger (1975)
	75	25	300	Welch and Kalff (1975)
	60–76	57	227	Present study
Norwegian Sea (Coastal)	69	—	1120	Thorndsen and Heimdal (1976)
Pacific				
Mid-subarctic	45–55	—	150–250	Koblenz-Mishke (1965)
		21	400	Larrance (1971)
Bering Sea (Coastal)	55–65		460	Taguchi (1972)
(Open water)			330	
		—	340–630	Taniguchi (1969)
		76	240	McRoy et al. (1972)
Arctic				
Chukchi Sea	70	128	990[b]	Hameedi (1978)
Beaufort Sea	71	—	280	Alexander (1977)
Barents Sea (Coastal)	70	31	304	Yedernikov and Solov'yeva (1972)
Arctic Basin	80–87	25	5–6	English (1961)

[a]Computed from annual production of 559g C·m^{-2} and 120-d growing season.
[b]Production per half-day (noon to sunset incubation).

noticeably lower than values found in most coastal areas (Table 3). Production rate normalized to chlorophyll *a* (photosynthetic index, P.I.) can be viewed as an indicator of phytoplankton turnover rate. The mean P.I. computed for all arctic waters (up to 80°N) combined was 6.7 g $C \cdot (g\ Chl)^{-1} \cdot d^{-1}$ as compared to our mean value of 4.0 for Baffin Bay (see Fig. 4). For the Arctic Basin, the value would be 0.2.

El-Sayed and Turner (1977) have recently summarized primary production data collected over the past several years in the Antarctic. They found that mean conditions for the Atlantic, Pacific, and Indian Ocean sectors combined were 17.4 mg $Chl \cdot m^{-2}$ and 134 mg $C \cdot m^{-2} \cdot d^{-1}$, integrated over the euphotic zone. This converts to a P.I. of 7.7 g $C \cdot (g\ Chl)^{-} \cdot d^{-1}$, a value somewhat higher than the arctic mean.

Generally speaking, most open-water areas in the Arctic (with the obvious exception of the Arctic Ocean Basin) appear at least as productive as the Antarctic during summer. Our data, as well as those of others (e.g. Welch and Kalff 1975), suggest that this is the case for Atlantic as well as Pacific arctic waters.

Nutrient Dynamics

The limited data on nutrient (nitrogen) assimilation rates in arctic waters (McRoy et al. 1972; Hattori and Wada 1974) have suggested that nitrate is the predominant source of inorganic nitrogen used (Hattori and Wada 1974, Fig. 6.2). In the Bering Strait, for example, McRoy et al. (1972) observed that nitrate accounted for 89% of the nitrogen assimilated by near-surface phytoplankton. For adjacent waters, however, the ratio (f) of NO_3^- uptake/total ($NO_3^- + NH_4^+$) uptake was closer to 0.50. For the eastern Canadian Arctic, (f) values averaged 0.53 (Table 2, last column) and exceeded 0.50 at only 4 of the 12 stations studied. Similar ratios have been found in the Antarctic (Olsen 1980). It is clear from these results that half the nitrogen required for arctic (and antarctic) primary production must be supplied by in situ nutrient regeneration (Dugdale 1967; Harrison 1980). This conclusion is further strengthened by our observations of (f) values averaging 0.43 in the productivity maximum layers. At the bottom of the euphotic zone (Chl max layer) for most stations, (f) averaged 0.60.

A number of studies have shown that PO_4^- concentrations in the eastern Arctic are generally high throughout the year, even when nitrogen (and to a lesser degree ($Si(OH)_4$) concentrations are reduced during the summer phytoplankton growth period (Grainger 1975; Welch and Kalff 1975; Jones and Coote 1980). Previously published work on phosphorus assimilation by arctic phytoplankton have been difficult to find. Our work has shown that PO_4^- is consumed in significant quantities by the phytoplankton in Baffin Bay. In fact, the rate of PO_4^- uptake appears significantly higher (relative to carbon and nitrogen uptake) in these populations than has been observed in temperate and tropical regions. For example, the mean assimilation ratios for the present study were 22 C:6 N:1 P as compared to temperate coastal values of 127 C:16 N:1 P (Harrison et al. 1977) and oligotrophic, open-ocean values of 62 C:9 N:1 P (Perry and Eppley 1981). We do not presently have data to confirm if the disproportionate PO_4^- uptake is reflected in the organic P content of the particulate matter.

Environmental Control of Arctic Primary Production

Dunbar (1968) has argued that arctic phytoplankton have probably adapted to their unique light and temperature environments, and that nutrients (or their absence) in the upper-water column determine productivity levels.[1] The chemical and physical environment described by Dunbar was typical of the stations we studied in Baffin Bay in 1978 and in the previous year (Jones and Coote 1980). Furthermore, concentrations of dissolved inorganic nutrients in the mixed layer revealed an abundance of PO_4^- and $Si(OH)_4$ and shortage of nitrogen. Nutrient assimilation ratios suggested that PO_4^- was utilized more rapidly (relative to nitrogen) than is typical for more southern latitudes. Yet, when assimilation and concentration ratios were compared (RUI, Fig. 6), it was apparent that nitrogen resources could be exhausted much more rapidly than PO_4^-.

Although nitrogen is probably the limiting macronutrient resource, neither results from our C:N particulate nor C:N assimilation ratios suggested severe nitrogen limitation. In fact, the assimilation ratios averaged slightly lower than the Redfield et al. (1963) ratios of 6.6:1, suggesting little or no nutrient stress (Goldman et al. 1979). Carbon:nitrogen assimilation ratios in nitrogen-depleted surface waters can exceed 20:1 (Eppley et al. 1979). McRoy et al. (1972) and Hattori and Wada (1974) found C:N assimilation ratios in the Bering Sea and adjacent water of 12:1 on the average. In the Antarctic, assimilation ratios ranged from (0.1−25.1) to 1 (Slawyk 1979). Slawyk found that assimilation and particulate C:N ratios were generally comparable for samples taken from between the 1 and 4% light depths. In our work, comparable ratios occurred between the 25 and 50% light depths (Fig. 7). Generally low C:N assimilation ratios (and particularly low at the bottom of the euphotic zone) emphasize the significantly weaker light dependence of nitrogen assimilation compared to carbon (see also Slawyk 1979 and Olsen 1980).

Recently, Eppley and Peterson (1979) have suggested that annual primary production can be calculated from the ratio of NO_3^- assimilation:total − N assimilation for waters where nutrients limit production. The relationship is: Total production (g $C \cdot m^{-2} \cdot yr^{-1}$) = ($f$)/0.0025 and is valid to ~ 250 g $C \cdot m^{-2} \cdot yr^{-1}$. Using a mean ($f$) of 0.47 (our mean f, Table 2, adjusted for the uptake of urea and other reduced N forms), the predicted annual production for Baffin Bay would be 188 g $C \cdot m^{-2} \cdot yr^{-1}$, a value nearly double the estimates presently available (Steeman-Nielsen 1958; Grainger 1975; Welch and Kalff 1975). Sharp et al. (1980) have also shown a similar relationship between growth rate and (f) value. Using their equation ($\mu\ (d^{-1}) = 0.97(f) + 0.11$), average growth rates from our study (as doublings $\cdot d^{-1}$) should be 0.40, which is greater than our euphotic zone mean of 0.31 doublings $\cdot d^{-1}$. These results suggest that environmental factors other than nutrient availability (light, temperature, etc.) are important in regulating Baffin Bay phytoplankton production and growth rate.

We observed that some of the variability in P.I. could be attributed to daily variation in incident solar radiation (Fig. 4), and that they were significantly correlated (Fig. 9). Larrance (1971) and Holm-Hansen et al. (1977) have observed similar correlations between euphotic zone production and incident radiation in arctic and antarctic waters. The

[1]In Dunbar's discussion, "Arctic" was intended to apply principally to the central Arctic Basin.

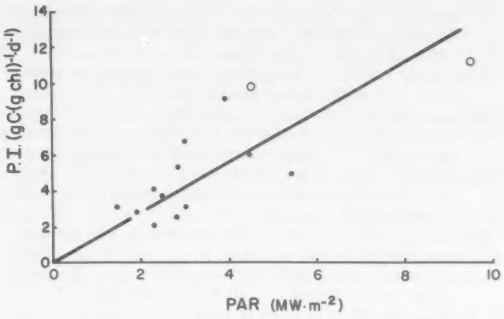

FIG. 9. Relationship between photosynthetic index (P.I.) and incident solar radiation, all cruise stations (Stn. 1–93). Solid circles represent Baffin Bay stations. Total radiation values were reduced by 10% (surface reflection) and divided by 2 to approximate photosynthetically active radiation (PAR). Regression line filled through origin (Snedecor and Cochran 1967).

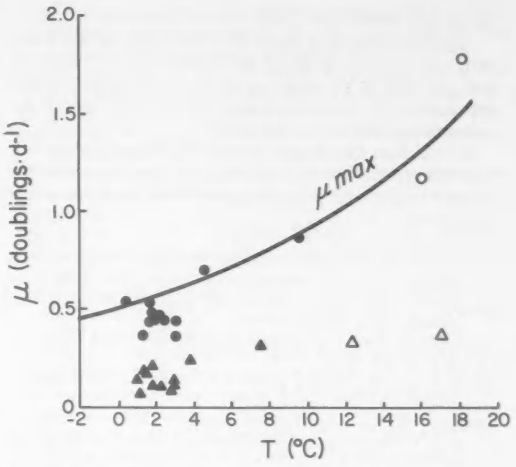

FIG. 10. Relationship between phytoplankton growth rate and incubation temperature, all cruise stations (Stn. 1–93). Curve represents theoretical maximum (μ_{max}) from Eppley (1972). Circles represent growth rates computed from assimilation numbers (A.N.) of Fig. 4. In this case, hourly rates were converted to daily rates by multiplying by 14. Triangles represent growth rates computed from mean in situ production rates of Table 2 (column 5). Filled symbols represent Baffin Bay stations. Growth rate computations given in text.

slope of this relationship (ψ) can be considered as an index of light utilization efficiency for photosynthesis in the euphotic zone (Falkowski 1981). In our study, ψ was 1.34 $\mu g\ C \cdot (g\ Chl)^{-1} \cdot (W \cdot m^{-2}) \cdot d^{-1}$ when all cruise stations were considered and 1.39 for stations north of 60°N. Both values of ψ were lower than are typical for temperate latitude coastal waters which range from 1.86 to 3.25 $\mu g\ C \cdot (g\ Chl) \cdot (W \cdot m^{-2}) \cdot d^{-1}$ (Patten 1961; Malone 1976; Platt and Irwin 1979; Falkowski 1981). Larrance (1971) did find a relatively high ψ value (2.67) in the mid-subarctic Pacific. Clearly, the phytoplankton populations we studied showed no special adaptive response (through increased light utilization efficiency) to the relatively low incident radiation to which they were exposed. In fact, they appeared to perform less well than their temperate counterparts.

Reduced compensation light intensities (where net photosynthesis = zero) have been suggested as an adaptive response of phytoplankton growing in low light and temperature environments typical of polar seas (Fogg 1977). The average compensation intensity derived from Baffin Bay primary production and light penetration data was found at the 0.8% light depth, or ~6.3 $W \cdot m^{-2}$ (using a mean daily irradiance of 3.5 $MW \cdot m^{-2}$, PAR). This value is lower than the I_c for cultured temperate diatoms 15.3 $W \cdot m^{-2}$ (Jenkins 1937) but much higher than Bunt (1964) found in antarctic phytoplankton populations 0.1–0.2 $W \cdot m^{-2}$. Holm-Hansen et al. (1977) often found compensation intensities below the 0.1 and 0.01% light levels in the Antarctic.

Eppley (1972) has shown that in the absence of light or nutrient limitation, phytoplankton maximum growth rates ($doublings \cdot d^{-1}$) can be expressed as a function of temperature for cells grown in continuous light [$\log (\mu_{max}) = 0.0275\ (°C) - 0.070$]. Growth rates, computed based on a 14:10 light/dark cycle using 50% light level assimilation numbers (A.N. = light-saturated photosynthetic rate, ref. Fig. 4) and average euphotic zone production rates (simulated in situ values), were plotted against incubation temperatures (Fig. 10). Growth rates computed from A.N. closely followed Eppley's growth–temperature relationship when all stations (45° to 76°N) were considered. Assimilation number growth rates for Baffin Bay stations averaged 85% μ_{max}, but were not significantly different. Despite the uncertainties in extrapolating this relationship to the low temperatures typical of Baffin Bay, these results do demonstrate the marked difference in potential growth rate between arctic and temperate phytoplankton populations and emphasize the importance of temperature in setting this upper limit. Similar observations have been made in the Antarctic (Holm-Hansen et al. 1977; Slawyk 1979; Olsen 1980).

Deviations of the measured growth rates from the predicted μ_{max} could be viewed as an index of the importance of environmental factors other than temperature in limiting growth rate (e.g. light, nutrients). In Baffin Bay, the similarity between A.N. growth rates (growth at optimum light) and the predicted μ_{max} suggests that nutrient limitation did not substantially depress the measured growth rates when compared to growth under optimal environmental conditions. On the other hand, growth rates measured under environmental light conditions (in situ estimates) were consistently below the predicted maximum ($\bar{x}$ = 52% μ_{max}) and suggest that light may be more important than the paucity of nutrients in regulating the growth of eastern Canadian Arctic phytoplankton.

Concluding Remarks

New data for Baffin Bay and a review of additional data from the eastern Canadian Arctic and Pacific Arctic/sub-Arctic suggest that these waters are more fertile from the perspective of the primary producers than previously believed. Similar studies in the Antarctic have recently shown that the annual production estimates for both polar environ-

ments now appear to be more closely equivalent.

Although nitrogen is nearly depleted in the surface waters in the Arctic during much of the phytoplankton growing season, only half of the requirements for phytoplankton growth appear to be dependent on vertical diffusion processes. In situ regeneration supplies the balance.

Several lines of evidence have been presented which suggest that temperature and light may be more important than nutrient limitation in regulating eastern Arctic phytoplankton production.

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NOTES

Temperatures Selected in a Power Plant Thermal Effluent by Adult Yellow Perch (*Perca flavescens*) in Winter

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ROSS, M. J., AND D. B. SINIFF. 1982. Temperatures selected in a power plant thermal effluent by adult yellow perch (*Perca flavescens*) in winter. Can. J. Fish. Aquat. Sci. 39: 346–349.

Winter-temperature selection by yellow perch (*Perca flavescens*) was monitored by radio telemetry near the thermal discharge from a power plant on the Upper Mississippi River. Ten fish were equipped with temperature-sensing radio transmitters. Temperature selection was monitored with an automatic recording system and manually with standard radio frequency receivers. The selected mean winter temperature for all locations was 5.4°C; when fish were in the discharge area mean temperature selected was 6.3°C. Ninety-one percent of the temperatures was recorded from fish in the discharge bay. Response to temperature varied greatly among individual fish, and they selected significantly lower temperatures in the field than in laboratory experiments. These field-selected temperatures correspond closely to those required for gametogenesis and spawning success in this species.

Key words: *Perca flavescens*, thermal requirements, radio telemetry, temperature selection

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La télémétrie par radio a été utilisée pour suivre la sélection des températures hivernales par la perchaude (*Perca flavescens*) près de l'effluent d'une centrale électrique du Haut-Mississippi. Dix poissons ont été équipés d'émetteurs radio sensibles à la température. Le choix de la température a été suivi à l'aide d'un système d'enregistrement automatique et manuellement avec récepteurs radio standard. À tous les endroits, la température hivernale moyenne choisie a été de 5,4°C; dans la région de l'effluent, cette température a été de 6,3°C. Quatre-vingt-onze pour cent des températures ont été enregistrées chez des poissons se trouvant dans la baie de l'effluent. La réponse à la température diffère beaucoup d'un poisson à l'autre. En outre, la température choisie sur le terrain est nettement inférieure à celle observée dans des essais de laboratoire. Ces températures choisies sur le terrain correspondent étroitement à celles requises pour la gamétogénèse et le succès de la ponte chez cette espèce.

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YELLOW perch (*Perca flavescens*) has evolved in a north-temperate environment. Its native distribution includes the northeast and north-central United States and most of central and eastern Canada (Scott and Crossman 1973). In most of this area ice cover and temperatures in the 0–4°C range occur during the winter season. Yellow perch are a popular sport and commercial fish in many areas, and, perhaps more importantly, this relatively small species is a principal component in the food web of game fish such as the walleye (*Stizostedion vitreum vitreum*) and northern pike (*Esox lucius*) (Maloney and Johnson 1955; Seaburg and Moyle 1964; Dobie 1966).

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The temperature preference of yellow perch varies with age, season, and acclimation. Ferguson (1958) reported that temperature acting alone determined the distribution of fish in a laboratory tank. He found that yellow perch preferred a temperature of 24.2°C in laboratory tanks and a temperature from 19.7 to 21.1°C under natural conditions. McCauley and Read (1973) pointed out that adult perch select a temperature that is ~ 3°C lower than that selected by juveniles. This difference was also noted by Barans and Tubb (1973), who further concluded that yellow perch temperature selection changed seasonally, and adult fish had a winter-temperature preference of 12–16°C. McCauley (1977) showed that the temperature preference of adult yellow perch changed with acclimation regardless of season. At 5°C acclimation, mean selected winter temperatures ranged from 12 to 14°C.

These relatively high preferred winter temperatures exceed the temperature of north-temperate waters under normal winter conditions. In addition, these temperatures are considerably above those noted by Jones et al. (1977) for successful gametogenesis. In laboratory studies they found that yellow perch reproduction was impaired when winter temperatures were higher than 4°C, or the period at 4°C was less or greater than 185 d. Hokanson (1977) reported the greatest percentage of female yellow perch spawned after a chill duration of 160 d at 4 and 6°C. He found substantial decreases in spawning as the chill temperature was increased to 8 and 10°C or as the period was reduced from 160 d. These controlled experiments suggest that adult perch prefer unnaturally high winter temperatures and that this selection might lead to a decrease in reproductive success.

The purpose of this study was to examine winter-temperature selection by yellow perch under natural conditions to determine the significance of laboratory-determined temperature preferences relative to fish movement and behavior near complex thermally altered environments. Temperature-sensitive radio telemetry was used because it was necessary to identify individual fish and collect information over time in a thermal effluent subject to variation induced by weather and changes in power plant operations.

Study area — Studies were conducted near Minnesota Power and Light Company's Clay Boswell Steam Electric Station on the upper Mississippi River in north-central Minnesota. The Clay Boswell Station uses river water for "once-through" cooling of two 75-MW generating units resulting in a design ΔT of 15°C. Discharge temperatures ranged from 3 to 18°C and averaged 14.5°C during this study. Heated water is discharged at the rate of 3400 L/s via a 442-m × 15-m canal into the northeast bay of Jay Gould Lake. This 12.9-ha, 7-m-deep bay is thermally isolated from the remainder of Jay Gould Lake by the Mississippi River, which flows past the mouth of the discharge bay and, until contact with heated water, is essentially isothermal at 0°C during winter months.

Methods — Yellow perch were collected with trap nets in the discharge bay. Fish selected for radio tagging were usually held less than 6 h in a temperature-controlled outdoor holding tank adjusted to approximately the temperature of the capture location. Individually distinguishable radio frequency (53 MHz) transmitters were mounted subdorsally (Winter et al. 1978) without anesthetic. After a 2- to 4-h recovery period, fish were returned to the capture site and released.

Temperature-sensing radio frequency transmitters were designed and constructed by the University of Minnesota Cedar Creek Electronics Laboratory. The spacing between transmitter pulses varied with temperature, but the pulse width remained constant. Transmitters averaged 4.6 cm long × 1.2 cm wide × 0.9 cm deep and weighed 4.9 g in water. Initially transmitters had a life expectancy of 100–120 d but a recording range of only 150 m. Current drain on later model transmitters was increased to achieve a recording range of ~ 0.7 km with a decrease in life expectancy to 30–40 d. Before the fish were tagged, transmitters were activated for 24 h and then calibrated to the nearest 0.1°C in agitated water.

Temperature data were collected principally with an automatic receiving–recording system housed in a remote recording shed on the north shore of the discharge bay (Ross et al. 1979). The system consisted of a four-element yagi antenna with a 16-channel programmable 53-MHz radio receiver, a pulse-rate decoder, and a strip-chart recorder. The receiver was programmed to receive data from each transmitter (fish) at 4-min periods once every 64 min. The pulse decoder measured time to the nearest 0.1 s for 10 pulse intervals from a preprogrammed frequency, and these data were recorded on a Rustrak recorder. The entire system was powered by a 12-V automobile battery. When fish were beyond the range of the automatic recording system, a stop watch was used to time pulse rates.

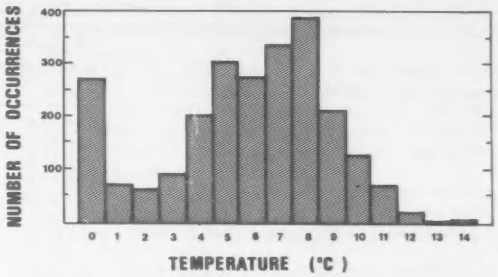

FIG. 1. Frequency distribution of yellow perch winter temperatures at all locations — January 1 to April 1, 1976.

Ten adult yellow perch were monitored for periods ranging from 7 to 62 d between January 1 and April 1, 1976. The average tracking period was 42 d. Temperatures of each fish were recorded on the strip charts to the nearest 0.1°C. Sampling intervals ranged from hourly to one temperature observation per day. Our goal was to obtain temperatures from individual fish each hour, but because of recording irregularities and fish movement out of the immediate area of the discharge bay, many individual fish were often monitored only once a day. The average frequency of observation was six temperature observations per fish per day. Ninety-one percent of the temperature observations were on fish in thermally altered waters. We attempted to monitor fish regardless of location until the transmitter expired.

Temperature data were analyzed in several ways with standard statistical programs (Nie et al. 1975). Mean temperatures were calculated for each fish with more than 15 observations. As some fish recorded better or for longer periods, individual means were then averaged so that each individual contributed equally to the group mean. To determine mean winter-temperature selection when perch were only in thermally altered waters, all temperature data greater than or equal to 1°C were analyzed by the same method presented above. Diel winter-temperature selection was determined by analyzing mean diurnal and nocturnal temperatures for those perch with more than 20 observations in each period. This analysis was performed on the data from all locations and discharge areas.

Results — The overall frequency distribution of yellow perch winter temperatures, that is, based on all data regardless of fish location or time of day, was bimodal with peaks at 0 and 8°C (Fig. 1). The lower mode reflects the large number

TABLE 1. Winter-temperature selections by yellow perch for all locations.

Fish no.	No. of observations[a]	Temp.[b] mean ± SD (°C)	Min. temp. (°C)	Max. temp. (°C)	95% confidence interval
1833	97	3.4±2.6	0	9.3	2.9–4.0
1834	160	5.0±3.0	0	12.8	4.5–5.5
1836	23	5.0±3.0	0	8.6	3.8–6.4
1837	1110	7.4±2.2	0	13.0	7.3–7.5
1838	342	4.8±2.9	0	12.9	4.5–5.1
1842	353	6.6±2.6	0	14.4	6.3–6.9
1843	92	1.1±1.8	0	10.1	0.7–1.5
1844	38	2.5±2.5	0	8.8	1.6–3.3
1847	29	9.2±4.3	0	14.6	7.6–10.9
1848	121	8.5±2.6	0	14.1	8.1–9.0

[a]Total number of observations = 2365.
[b]Mean for all fish = 5.4°C.

TABLE 2. Winter-temperature selections by yellow perch in thermally altered areas.

Fish no.	No. of observations[a]	Temp.[b] mean ± SD (°C)	Min. temp. (°C)	Max. temp. (°C)	95% confidence interval
1833	74	4.5±2.0	1.1	9.3	4.0–5.0
1834	130	6.2±2.0	3.9	12.8	5.8–6.5
1836	18	6.5±1.4	4.1	8.6	5.7–6.5
1837	1096	7.5±2.0	1.2	13.0	7.4–7.6
1838	274	5.9±1.9	1.1	12.9	5.7–6.2
1842	343	6.8±2.4	1.4	14.4	6.5–7.1
1843	35	2.8±1.9	1.2	10.1	2.1–3.4
1844	28	3.2±2.5	1.2	8.8	2.3–4.2
1847	25	10.7±2.4	6.9	14.6	9.7–11.7
1848	120	8.6±2.6	2.2	14.1	8.0–9.2

[a]Total number of observations = 2143 (91% of total observations).
[b]Mean for all fish = 6.3°C.

of temperature observations on fish that moved into unaltered waters. The 8°C mode represents the most commonly encountered temperature while yellow perch were in the discharge-affected areas. The mean temperature selection for all locations, determined by averaging individual means, was 5.4°C. Mean temperature selections for 10 individuals ranged from 1.1 to 9.2°C (Table 1). Analysis of variance indicated a significant difference among average temperature data for individual perch ($\alpha = 0.05$). The least significant difference and the Student–Newman–Kuels' procedure indicated that the winter temperature means with 20 or more observations per individual could be separated into seven different groups. The Scheffe procedure, a very conservative test, divided the individual overall winter means into four subsets with a maximum of four fish in a group, and one fish (1836) overlapped in two subsets.

Every fish resided in unaltered waters at least briefly as indicated by temperatures of 0°C recorded in Table 1. Winter-temperature selections by perch in the discharge area are presented in Table 2. Variability among individual fish remained substantial; means ranged from 2.8 to 10.7°C. The multiple comparison test with the Scheffe procedure separated the 10 individuals into five significantly ($\alpha = 0.05$) different subsets. The mean temperature selection for yellow perch in the discharge-affected areas determined by averaging individual means was 6.3°C.

Because of the high degree of temperature variability among the individual perch, winter diel temperature selection was examined on an individual basis. Diurnal and nocturnal temperature data were analyzed for all readings and for observations in the discharge area. A *t*-test on all individual perch, winter day and night mean temperatures indicated no significant ($\alpha = 0.05$) difference. When the data from the discharge area were analyzed separately, four of six individuals showed no significant difference in diel temperature selection, and the other two fish had diurnal means 0.7 and 0.6°C higher than nocturnal means.

Discussion — The effects of environmental disturbances on mobile organisms such as fish can be viewed as arising from cumulative dosage. Thus, thermal effects depend primarily on acclimatization history or the duration and intensity of exposure of fish to a heated effluent.

Yellow perch inhabiting the heated discharge selected relatively cool water from the 0–15°C gradient available and demonstrated a high degree of variability in mean selected water temperatures. The 5.4°C overall mean temperature for perch near the thermal discharge is within the 4–6°C chill period range that Hokanson (1977) reported as maximum for spawning and in the 50–75% range for viable eggs found by

Jones et al. (1977). In a previous study Ross and Winter (1981) found that the duration of yellow perch exposure to a thermal effluent was limited and almost always transitory. These data are significant in that whole populations are not automatically attracted to warmwater plumes. Ross and Siniff (1980) reported that spawning time and gonadosomatic indices were similar for yellow perch collected in the discharge bay and in thermally unaffected areas. Additionally, J. D. Winter (State University of New York unpublished data) hatched eggs from perch caught in the discharge bay, but did not measure egg viability. Apparently the thermal discharge had little if any effect on gametogenesis.

The temporal–spatial distribution of fishes in their natural habitat is the end result of a great number of contributing factors, each with its own direction and intensity of influence. The temperatures selected by yellow perch we observed in the field were lower (1.1–9.2°C) and less uniform than those observed by Barans and Tubb (1973) and McCauley (1977) in laboratory studies (12–16°C). These observations indicate that factors other than, or in addition to, temperature substantially influenced yellow perch spatial distribution in the field.

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Comparison of Two Sampling Methods for Estimating the Abundance and Distribution of *Mysis relicta*

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Vertical net hauls taken at night yielded a population estimate for *Mysis relicta* of 5 300 000 ± 1 060 000 ($P \leq 0.05$) while quadrat counts done by SCUBA divers in the daytime fixed the population size at 1 100 000 ± 170 000. Observations by divers suggested that the behavior and distribution of *Mysis* during the day resulted in an underestimate of their

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abundance by the quadrat method. Net hauls showed that at night mysids migrated both vertically to the base of the epilimnion and horizontally within the metalimnion. A vertical tow rate of $\frac{1}{3}$ m·s^{-1} used for the nighttime population estimates lay within the optimum sampling speed of the net. Repeated sampling at a single station had little or no effect on catch totals for up to nine consecutive hauls. Beyond this number some local depletion was noted. A modified vertical tow net which sampled on descent then closed once contact was made with the substrate performed no better than a standard net except when the shallowest stations were sampled repeatedly. Temporal variation in the catch of young-of-the-year *Mysis* at shallow stations, however, contributed at most ±8% error to the whole lake population estimate.

Key words: Mysidacea, diurnal migration, samplers, SCUBA, vertical net tows

NERO, R. W., AND I. J. DAVIES. 1982. Comparison of two sampling methods for estimating the abundance and distribution of *Mysis relicta*. Can. J. Fish. Aquat. Sci. 39: 349–355.

Des prises de plancton verticales effectuées la nuit donnent des estimations de population de *Mysis relicta* 5 300 000 ± 1 060 000 ($P \leq 0{,}05$) tandis que des comptages par quadrants faits par des plongeurs autonomes le jour donnent un effectif de population de 1 100 000 ± 170 000. D'après les observations des plongeurs, le comportement et la distribution des mysides le jour résulteraient en une sous-estimation de leur abondance par la méthode des quadrants. Les pêches de nuit démontrent qu'à ce moment-là les mysides émigrent à la fois verticalement vers la base de l'épilimnion et horizontalement dans le métalimnion. Une vitesse de trait vertical de $\frac{1}{3}$ m·s^{-1} utilisée dans les estimations de population la nuit se trouve dans les limites optimales de vitesse d'échantillonnage du filet. Un échantillonnage répété à une seule station n'a que peu ou pas d'effet sur les prises totales, jusqu'à concurrence de neuf traits consécutifs. Au-delà de ce nombre, on note quelque diminution locale. Un filet vertical modifié, capable d'échantillonner durant la descente, ensuite de se fermer une fois en contact avec le substrat, ne se comporte pas mieux qu'un filet standard, sauf quand les stations les moins profondes sont échantillonnées de façon répétée. La variation temporelle des prises de *Mysis* de l'année aux stations peu profondes contribuent cependant tout au plus ±8% d'erreur aux estimations de la population du lac entier.

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ESTIMATES of population size from sample data rely on two critical assumptions: first, that the sampling scheme takes into account the spatial distribution of the population and second, that the sampling gear provides unbiased estimates of density. If the animals are randomly distributed the first assumption is easily satisfied. Spatial heterogeneity can be overcome by a stratified sampling scheme; however, gear bias is often a more difficult problem to evaluate. The purpose of this study was to estimate the total number of *Mysis relicta* and the spatial distribution of this population in Lake 223 (L.223) at the Experimental Lakes Area, northwestern Ontario, by two independent techniques, then to examine each method for evidence of sampling bias.

The occurrence of *M. relicta* on or near the lake bottom during the daytime has led a number of workers to sample them by towing benthic sleds equipped with nets across the lake bottom (Beeton 1960; Reynolds and DeGraeve 1972; Grossnickle and Morgan 1979; Malley and Reynolds 1979). The small size of L.223 (27.27 ha), combined with extremes of bottom type found in the zone of *Mysis* occurrence (loose flocculent sediment or gravel interspersed with large boulders and granite outcrops), made sampling with a benthic sled impractical. Alternatively, daytime abundance estimates have been based on a series of quadrat counts done by SCUBA divers (Lasenby 1971). Quantitative samples of *Mysis* have also been taken at night when the *Mysis* population is planktonic by towing a net vertically through the water column (Hakala 1978; Morgan et al. 1978; Grossnickle and Morgan 1979; Malley and Reynolds 1979). Both daytime SCUBA counts and nighttime vertical net hauls were used and compared in this study.

Methods — Mysis abundance was determined as part of an overall study aimed at evaluating the response of L.223 to artificial acidification (Schindler 1980; Schindler et al. 1980).

Initial SCUBA surveys showed that during late August 1978 (the time of the population census), mysids were restricted to a region of the central lake basin between the top of the thermocline (5 m) and the upper boundary of the anoxic water in the hypolimnion (9 m). A total of 197 direct counts, by SCUBA divers, were made on cloudless days between August 29 and September 4, 1978, at approximately solar noon when the mysids were completely benthic. Between August 2 and August 27, 1978, 83 net hauls were made at least 1 h after sunset on moonless nights, the optimum light conditions for *Mysis* vertical migration (Beeton 1960; Nero unpublished data).

Before making diver estimates of mysid abundance, several sizes and types of quadrats were tested. Mysids avoided visible objects, escaped from open-frame quadrats, and were

displaced from the counting area by a bow wave when quadrat boxes with closed tops were placed on the substrate. The quadrat chosen for use was a clear, acrylic-plastic, square box (25 cm × 25 cm × 10 cm high) with an open bottom and a 5-cm-wide lip around the top inside perimeter. This partial top design proved to be the best compromise between bow wave effect and counting accuracy. An acrylic handle attached to one side of the quadrat allowed the diver to place it on the lake bottom ahead of him without shading the substrate or blocking water flow through the box with his hand. An underwater light was used to illuminate the counting area once the quadrat was in position. Mysids caught within the box swam near the substrate until they encountered one of the quadrat sides, whereupon they typically attempted an escape by darting upward. With their escape route blocked by the top inside lip of the box, mysids returned to the substrate allowing the diver sufficient time to make an accurate count. Divers used a two-way voice communications system to relay counts and detailed observations to a surface attendant for recording.

A depth-stratified counting scheme (Elliott 1973) with 0.3 m of depth per stratum was used by the divers over the zone of *Mysis* occurrence. Several replicate counts were made within each stratum along six transects perpendicular to the shore spaced at regular intervals around the central lake basin. Within a given stratum samples from all transects gave similar densities (Friedman test, $P = 0.18$, Hollander and Wolfe 1973).

Vertical net hauls were used to determine the nighttime abundance of *Mysis* in the water column. Samples were collected along six transects, arranged in a similar manner to those used for the SCUBA estimates. Catch in each sample was expressed as total mysids per square metre. A poststratification technique was used to segregate samples, on the basis of total column depth, into five 1.5-m strata over the depth range 5−12.5 m and one 1.9-m stratum (12.5−14.4 m).

The vertical tow net was shaped like an inverted pyramid (basal opening 1 m × 1 m) with sides tapering towards the end in two stages. Coarse mesh (1 mm × 1 mm opening) converged to an apical diameter of 22 cm, 1 m below the mouth of the net. To the apex was attached a ½-m-long cod end of 210-μm-mesh Nitex® cloth which terminated in a plastic fitting equipped with a rubber drain tube, held closed by a pinch clamp. The combination of two mesh sizes permitted the user to haul the net vertically at a reasonable rate with a minimum bow wave while assuring that *Mysis* swept into the cod end suffered little damage from the net and could easily be removed. Lines from each corner of an aluminum support frame at the mouth of the net formed a bridle with a central attachment to a single tow rope. Based on the results of preliminary tests, we used a bottom time of 30 s to 1 min before retrieving the net and a towing speed of $\sim \frac{1}{3}$ m·s^{-1} for optimum results.

Differences between population estimates derived from SCUBA counts and net hauls subsequently led to a more detailed investigation of the sampling characteristics of the net. Because of a drastic reduction of the *Mysis* population size in L.223 over the winter of 1978−79, probably as a result of experimental acidification (Nero unpublished data), net performance tests were conducted in nearby Lake 239 (L.239) in 1979 and 1980. A physical description of L.239 is available in Brunskill and Schindler (1971).

To evaluate the effects of repetitive sampling, several replicate total column samples were taken over a ½-h period at each of five sample stations (depths: 6, 9, 14, 23, and 30 m).

To determine whether or not vertical haul rate affected the catch efficiency of the net, three replicates of four hauling speeds ($\frac{1}{6}$ m·s^{-1}, $\frac{1}{4}$ m·s^{-1}, $\frac{1}{2}$ m·s^{-1}, and $\frac{3}{4}$ m·s^{-1}) were tested in random sequence at the 14-m station.

Additional tests were conducted as paired comparisons between the vertical tow net and a downward-sampling closing net to determine whether or not catches varied as a result of mysids being: (i) trapped beneath the vertical tow net as it was lowered into position, (ii) attracted or repelled by sediment stirred up when the net contacted the lake bottom, or (iii) influenced by vibrations or bow wave effects from the towing bridle as the sample was taken.

The closing net was similar in design to the vertical tow net except that it sampled from the lake surface to the bottom, then closed. The descent line was attached to four cords which passed through a weighted aluminum frame and were attached to the net. Tension on the cords from the weight of the frame held the net open. Rate of fall through the water column could be regulated from the surface by the descent line. Once bottom contact was made the descent line was slackened. A second rope from the surface, used for retrieval, functioned as a drawstring to close the mouth of the net. Performance tests were conducted at eight depths (5.9, 7.0, 9.4, 9.6, 13.6, 13.7, 13.8, and 29.9 m) in L.239 on eight nights between June 24 and September 3, 1979, by sampling alternately with each net design.

Using the standard net design the vertical distribution of *Mysis* in the water column was determined on July 1, July 8, and September 3, 1979, in L.239 at the 5.9-, 13.6-, and 14.8-m stations, respectively. The number of *Mysis* in progressively deeper 1-m^3 volumes of water were determined by subtracting the number caught from z-m depth from the number caught at $z + 1$ m depth.

Sample catches from each of the net-test experiments were enumerated as young-of-the-year or adult mysids based on measurements of total animal length (<10 and ≥10 mm, respectively). Information on oxygen and temperature profiles for the lakes was furnished by D. W. Schindler (Freshwater Institute, Winnipeg).

Results and Discussion — During the daytime the entire *Mysis* population was benthic (Fig. 1A). The shoreward limit of *Mysis* occurrence was marked by the top of the thermocline (17.6°C) while the lower limit of their distribution coincided with a region of the lower metalimnion where oxygen concentrations dropped from 10.2 mg·L^{-1} at 8 m to 0.3 mg·L^{-1} at 10 m. No mysids were found outside these limits.

At night, *Mysis* in the water column moved horizontally to cover a larger portion of the central lake basin (Fig. 1B). The limit of their shoreward occurrence remained the same as in the daytime. Observations made using SCUBA at night showed that mysids remained above the anoxic waters of the hypolimnion. Differences between daytime and nighttime distribution patterns suggest that each night mysids migrate vertically and horizontally (2 m vertically and on average 50 m horizontally) away from the areas of maximum daytime density while staying within physiologically tolerable conditions in the water column.

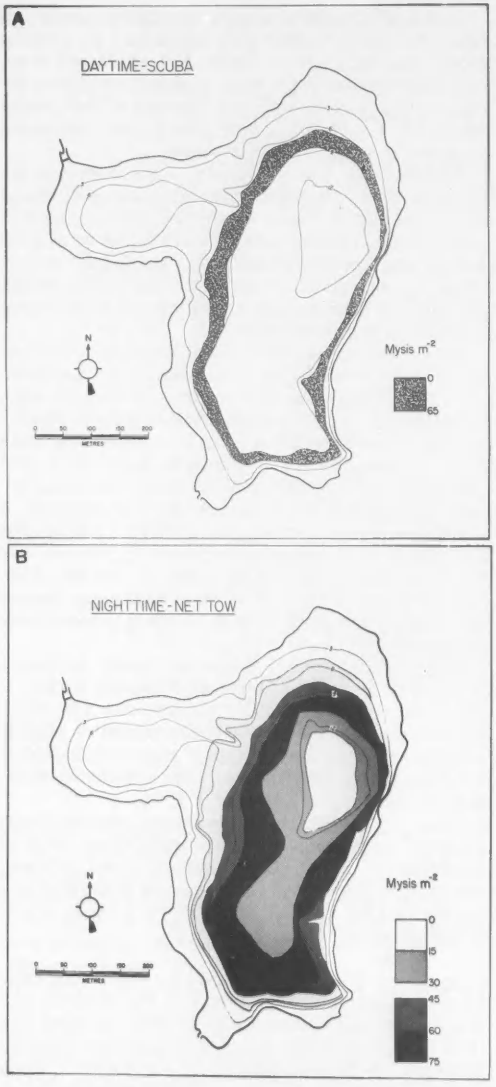

FIG. 1. *Mysis relicta* densities in L.239 for (A) daytime densities on the lake bottom obtained from quadrat counts for August 29 to September 4, 1978, and (B) nighttime densities within the water column obtained from net hauls August 2 to August 27, 1978. Depth contour interval is 3 m.

Although the two census methods gave reasonable information on the relative distribution of *Mysis* in the lake during the day and at night, they did not compare favorably when used to construct population estimates. Data from the diver-taken quadrat counts fixed the total population at 1 100 000 ± 170 000 (95% confidence limits) while the net haul method gave a significantly different estimate ($P \leq 0.01$) of 5 300 000 ± 1 060 000.

This discrepancy between abundance estimates could not be attributed to anything other than methodological differences. Water samples taken from depths corresponding to the zone of *Mysis* occurrence on July 31, August 28, and September 25 showed a pH change of only 0.2 units from 6.3 to 6.1, well above a value of 5.9 recorded in May of the same year. During the experiment the lake was thermally stratified with the thermocline slowly declining 1 m between July 31 and September 25. Oxygen concentrations during the same period remained constant at 10 $mg \cdot L^{-1}$ and 0.4 $mg \cdot L^{-1}$ for the 8- and 10-m depths, respectively. No evidence of a temporal decline of the *Mysis* population, beyond the 10% expected from considerations of life history (Hakala 1978), could be found in the data from either method. Less than 30 h elapsed between the final net tow sampling and the onset of the quadrat counts. Because lake conditions were stable during this brief interval between sampling periods, a catastrophic population failure could not account for the observed discrepancy in abundance estimates.

Several sources of error may have acted to give an artificially low value to the quadrat estimates of abundance. Even though divers made extensive observations which showed that during the day mysids were completely benthic and present only between 5 and 9 m, within that zone *Mysis* tended to aggregate around boulders, rock outcrops, and in areas of cobbles where often a quadrat could not be effectively placed. The rocky nature of the bottom together with the fact that portions of it are overlain by plate-like ferromanganese deposits, frequently undercut by tunnels and cavities, raises the possibility that a substantial portion of the mysid population remained hidden from view as suggested by Lasenby (1971). Mysids also tended to swim away from divers and the quadrat. Despite careful quadrat placement, some *Mysis* were occasionally displaced by its bow wave. Because few of the above errors could be easily quantified, we turned instead to a detailed examination of the net haul method.

Efficiency factors aside, vertical net tows should give reasonable estimates of abundance provided that the population sampled is entirely planktonic. At night the catch of a series of net hauls taken from progressively deeper starting points at a deep station showed that mysid abundance was maximum within the metalimnion (Fig. 2A). The same station sampled 2 mo earlier during full moon gave similar results except that a second peak of *Mysis* occurred at the bottom (Fig. 2B). This lower peak is probably due to an inhibition of their vertical migration by moonlight (Beeton 1960; Bowers and Grossnickle 1978; Morgan et al. 1978). At a shallow station sampled on a moonless night, most *Mysis* were confined to the lower 2 m of the water column by the presence of the thermocline 1.7 m above the bottom (Fig. 2C). Observations using SCUBA on moonless nights confirmed that mysids were only seen near the bottom in the zone where the thermocline contacted the substrate.

Tests of relative catch size vs. towing speed of the net (Fig. 3) showed that a vertical tow rate of $\frac{1}{2}$ $m \cdot s^{-1}$ used for the population estimates lay within the range of optimum sampling speeds for the net. For a haul rate of $\frac{3}{4}$ $m \cdot s^{-1}$ the catch was significantly less ($P \leq 0.05$, Friedman test, Hollander and Wolfe 1973) than at lower speeds. At the highest towing speeds resistance to water flow through the net created a

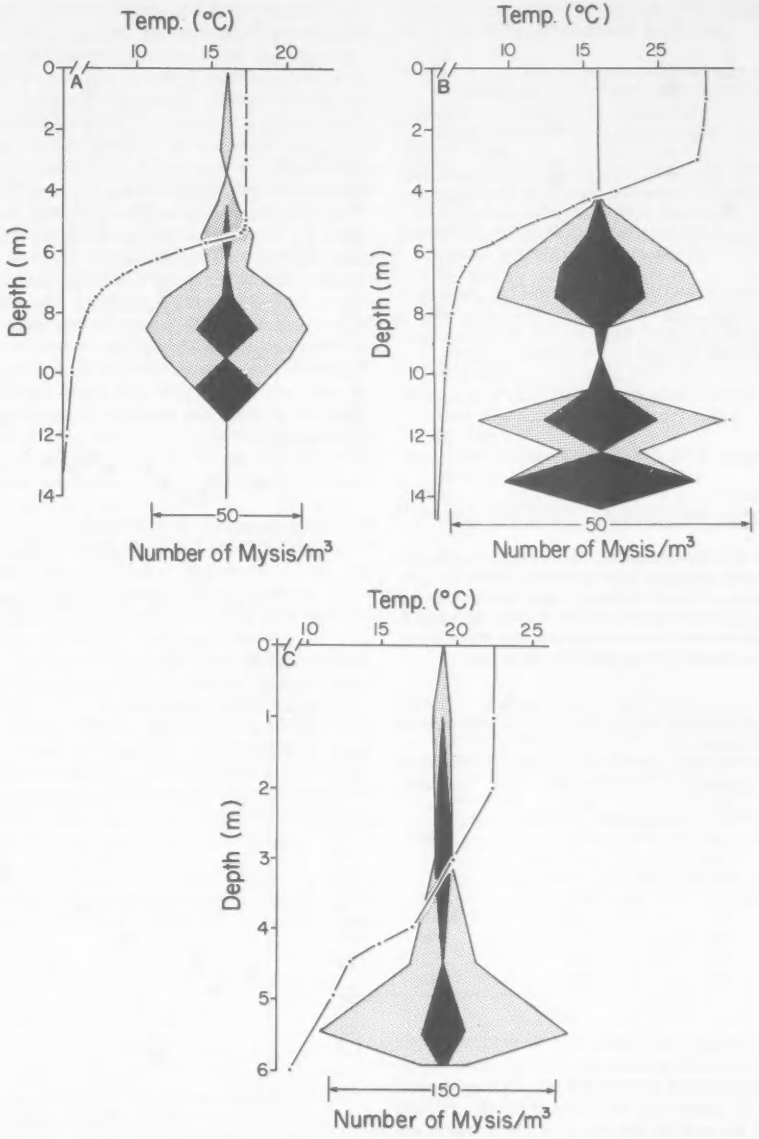

FIG. 2. (A) Vertical distribution of *Mysis relicta* with depth in L.223 on September 3, 1979 at a 13.6-m station. Total catch at each depth has been subdivided into young-of-the-year (light shading), and adults (dark shading). The temperature profile is shown by the broken line. (B) similar to (A) except that a 14.8-m station was sampled on July 8, 1979, during full moon. (C) A shallow 5.9-m station sampled on July 1, 1979.

substantial bow wave which displaced mysids away from the net mouth resulting in a reduced catch. We found no evidence of net avoidance behavior even at the slowest hauling rates. Similarly, Fleminger and Clutter (1965) showed that nighttime avoidance of nets by marine mysids was marginal. The lowest catches (Fig. 3) were obtained for the last 3 hauls in a series of 12 suggesting that local depletion of *Mysis* may have occurred as a result of repeated sampling over a short period of time.

A single pair of samples from each of eight stations was

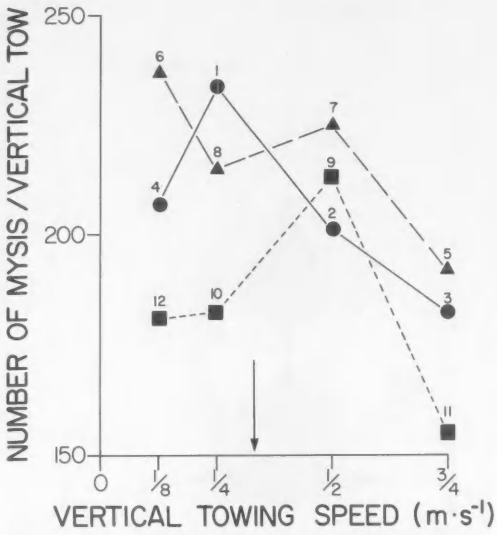

FIG. 3. Number of *Mysis relicta* caught in a vertically towed net at various towing speeds on July 6, 1980 at a 14-m station in L.239. Lines and symbols denote blocks containing a random arrangement of the four sampling speeds (●, block 1; ▲, block 2; and ■, block 3). Sampling order is indicated by the numbers above the symbols. Arrow indicates speed used during sampling experiments.

TABLE 1. Total catch of *Mysis relicta* from a standard vertical tow net and a downward sampling-bottom closing net from eight trials in Lake 239 during summer 1979.

	Depth (m)	Standard net	Downward net
June 24	13.8	98	75
July 1	5.9	123	160
Aug. 15	7.0	41	36
Aug. 21	13.7	108	124
Aug. 26	9.4	94	97
Sept. 2	9.6	176	126
Sept. 2	29.9	104	72
Sept. 3	13.6	150	181

used to compare the catch performance of the vertical-tow net and a downward-sampling closing net. Overall, there was no significant catch difference between the two net types (paired *t*-test, $P = 0.80$), indicating that even if mysids became trapped beneath the vertical tow net as it was lowered into position prior to taking a sample, or if their behavior was influenced by the rope-towing bridle, these factors did not bias the relative catch characteristics of the tow nets (Table 1).

For shallow stations, where mysid vertical migration was restricted to a narrow range of depth by the upper boundary of the thermocline (Fig. 2C), the number of young *Mysis* caught per haul increased as sampling continued (Fig. 4A). The increases may have been due to a temporal variation in the abundance of *Mysis* at the stations. Alternatively, changes may have been brought about by repeated sampling. Both

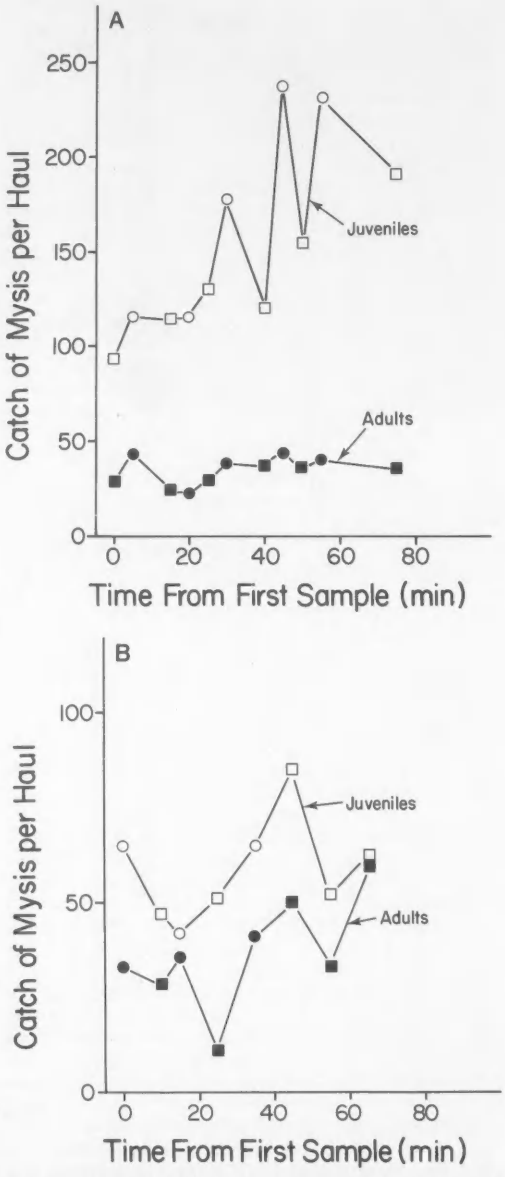

FIG. 4. (A) Catch of *Mysis relicta* for consecutive hauls of a vertically towed net (squares) and a downward sampling net (circles) at a 5.9-m station in L.239 on July 1, 1979 (moonlit night). (B) Similar to (A) except that a 13.6-m station was sampled on June 24, 1979 (moonless night).

nets may initially undersample the young, but as sampling continued young *Mysis*, previously located near the substrate, moved into the water column and became available for

capture. Another possibility is that the initial samples were representative of the station, but as sampling continued young-of-the-year *Mysis* were attracted to the sediment cloud stirred up by each successive sampling resulting in an overestimate for the later hauls. For samples taken toward the end of the series, catches were higher for the closing net than for the vertical tow net. In addition, young-of-the-year *Mysis* made up a higher proportion of the catch in samples from the closing net. These differences suggest that vertical tows may undersample *Mysis* located near the bottom, particularly young-of-the-year, by trapping them beneath the net before each sampling haul. At deeper stations on moonless nights (Fig. 4B) where both adults and young are located higher in the water column, the discrepancy between the net catches was negligible. The importance of variation in the catch of shallow stations to a whole-lake population estimate is minor. For example, in L.239, if the two extremes in the abundance of young-of-the-year *Mysis* (Fig. 4B) are used to construct maximum and minimum population estimates for that lake, the final results differ by only 8%. A similar calculation for L.223 yields a 2% difference overall. The magnitude of this error varies among lakes depending on the population distribution and basin morphometry.

Determining *Mysis* abundance by diver-taken quadrat counts may be a useful method for lakes where the population is entirely benthic such as those at high arctic latitudes exposed to 24-h daylight (Lasenby 1971). In most cases, though, mysids avoid divers, remain hidden from view, or aggregate around rocks where quadrat placement is difficult, making net hauls at night a more attractive census technique. Except in the case where shallow stations are sampled, vertical net hauls taken on moonless nights appear to be free of avoidance and depletion effects caused by bow waves, interference from the towing bridle, or local reduction of the population in the water column from replicate sampling, and as suggested by Malley and Reynolds (1979) and Grossnickle and Morgan (1979), represent a reliable method for obtaining estimates of *Mysis* abundance in the water column.

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Rate of Gastric Evacuation for Winter Flounder, *Pseudopleuronectes americanus*

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The rate of gastric evacuation of winter flounder, *Pseudopleuronectes americanus*, calculated from the rate of hunger return (determined as the amount eaten voluntarily at some time following a satiation meal) at ~ 6°C was exponential and equaled 0.079 h^{-1}. Feeding voluntarily on small pieces of squid, the fish ate 1.8–2.4% of their body weight per day, the actual weight of food consumed varying directly with fish weight so that ln wt food (g) = −2.988 + 0.780 ln wet wt fish (g). Stomach volume also varied with fish weight: stomach vol (cm^3) = 0.923 + 0.039 wet wt fish (g). Preliminary estimates of daily ration using several independent models agree closely with laboratory measurements of daily consumption.

Key words: winter flounder, gastric, evacuation

HUEBNER, J. D., AND R. W. LANGTON. 1982. Rate of gastric evacuation for winter flounder, *Pseudopleuronectes americanus*. Can. J. Fish. Aquat. Sci. 39: 356–360.

L'évacuation du bol alimentaire de la plie rouge, *Pseudopleuronectes americanus*, calculée à partir du retour de la faim (déterminée comme étant la quantité de nourriture ingérée volontairement à un moment quelconque après un repas à satiété) à ~ 6°C se produit à un taux exponentiel et égal à 0,079 h^{-1}. Se nourrissant volontairement de petits morceaux d'encornets, les poissons mangent 1,8–2,4% de leur poids corporel par jour, le poids réel de nourriture consommée variant en fonction directe du poids du poisson, de sorte que ln poids de nourriture (g) = −2,988 + 0,780 ln poids humide du poisson (g). Le volume de l'estomac varie également en fonction du poids du poisson : volume de l'estomac (cm^3) = 0,923 + 0,039 de poids humide du poisson (g). Des estimations préliminaires de ration quotidienne obtenues à l'aide de plusieurs modèles indépendants s'accordent étroitement avec des mesures de consommation quotidiennes effectuées en laboratoire.

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QUANTITATIVE estimates of gastric evacuation and daily consumption as well as diet composition are necessary to develop multispecies assessment models for commercially exploited fishes. Considerable literature exists documenting prey of northwest Atlantic fish (Edwards and Bowman 1979; Langton and Bowman 1980, 1982; Grosslein et al. 1982), and several methods of calculating daily ration have been developed. The most recent ones either use stomach contents data from the field exclusively (Lane et al. 1979) or use these field data together with experimental laboratory studies on evacuation rates (Elliott and Persson 1978; Eggers 1979). At present, little quantitative information on gastric evacuation is available for marine species (see reviews by Kapoor et al. 1975; Fänge and Grove 1979).

Winter flounder, *Pseudopleuronectes americanus*, was selected as a test species as it is of commercial value and has a wide geographic range along the east coast of North America. Its basic biology including feeding habits is well studied (see review by Klein-MacPhee 1978), but the only attempt to document consumption by adult fish is a laboratory study by Tyler and Dunn (1976). The purpose of our work was to determine the rate of gastric evacuation of the winter flounder which could be used with appropriate models to estimate daily ration for this species.

Methods — Winter flounder were collected from Woods Hole Harbor in November 1979 with a small otter trawl. About 70 fish (ranging in size from 10 to 40 cm, ~ 10–500 g) were kept together in a tank (~ 1300 L) supplied with running Woods Hole Harbor seawater at ambient temperatures (5–7°C) for 6 wk before 24 individuals were transferred to separate cylindrical fiberglass tanks (60 cm diameter × 75 cm high, volume 190 L). During this initial 6 wk, the fish were fed small pieces of previously frozen squid every 1–2 d. The fish were fed squid once daily while

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adjusting to the individual tanks for 1 wk prior to the experiments. Water flowing through the tanks varied from 5.5 to 7°C and was completely replaced 3–4 times each day (flow rate 400–500 mL/min). Fish received a light–dark regime of 11L:13D where light was provided by a bank of fluorescent lamps and "darkness" consisted of dim light from six 25-W incandescent bulbs at some distance from the tanks.

For experimental feedings, squid was cut into 0.5- to 1-cm pieces, thoroughly thawed, then gently blotted and weighed. For treatment A, the fish were fed at 09:00–10:00 and were allowed to feed on a preweighed quantity of squid for ½–¾ h, after which the food remaining was removed, blotted, and weighed, and the amount eaten calculated. Observations indicated that the flounder ignored uneaten food after 10–15 min. Each fish was given more than it would consume during a single feeding period. The initial experiment of treatment A lasting 8 d consisted of allowing the fish to feed to satiation once every 24 h. Subsequent experiments in this treatment lasting 3–6 d each involved feeding the fish to satiation twice during a 24-h period with the second meal coming 2, 4, 6, or 12 h (time t) after the first (time t_0). The method is based on the assumption that the amount of food consumed at the second feeding (a measure of hunger return) is equivalent to the amount of food already digested from the previous meal; therefore, hunger recovery is directly related to gastric evacuation. Each fish was the subject for each experimental series for at least 3 consecutive days.

In a final experiment (treatment B), fish were fed to satiation and three or four individuals were anesthetized using MS222 (~ 0.5 g/L) and killed at 2, 4, 6, 12, 24, and 55 h after feeding. The fish were weighed to the nearest gram and measured to the nearest millimetre; food remains from the stomach and intestine were blotted and weighed to the nearest 0.01 g at each of the time intervals. The state of digestion and position of food along the intestine were noted. In addition, stomach volume was measured by clamping the stomach at the esophagus and pyloric sphincter, then filling it with water injected through a syringe needle as described by Kimball and Helm (1971).

Results — The weight of food consumed by winter flounder (using mean weight of food eaten when fish were fed at 24-h intervals) is related directly to fish weight in the following way:

$$\ln \text{ wet wt food (g)} = -2.988 + 0.78 \ln \text{ wet wt fish (g)} \quad (r = 0.88,\ n = 21)$$

or

$$\text{wet wt food (g)} = 0.959 + 0.012 \text{ wet wt fish (g)} \quad (r = 0.69,\ n = 21).$$

Consumption expressed as percent body weight eaten per day (based on feedings at 24-h intervals) averaged 2.4% of body weight in all but the largest (>300 g) fish where it fell to 1.8% body weight per day. Several of the larger (>200 g) fish, excluded from this calculation, failed to feed during the experiments, probably as a result of prespawning fasting.

Stomach volume was related exponentially to fish length and linearly to fish weight. The following equation describes the relationship between stomach volume and fish wet weight:

$$\text{Stomach vol (cm}^3\text{)} = 0.923 + 0.039 \text{ fish wet wt (g)} \quad (r = 0.89,\ n = 16).$$

Comparing the volume of squid consumed (1 g of squid = 0.94 cm^3) with stomach volume indicated that small fish tended to fill their stomachs while larger fish usually did not (Table 1).

Consumption varied among fish of similar size and from day to day producing a variable feeding pattern. This pattern may result from the fact that in the laboratory, at the temperatures used, the fish did not empty their stomachs completely once every 24 h (Table 2). This is supported by the time taken for hunger recovery and by the results of dissections at intervals after feeding. Several of the 24 fish had more in their stomachs than they ingested at the preceding meal, and one fish examined 55 h after feeding still had food in its stomach (Table 2).

Stomach content (expressed as a proportion of initial intake) decreased exponentially (Fig. 1). If the mean values of S_0 and S_t (stomach contents at time t_0 and t, respectively) at each time t are used to solve the equation for gastric evacuation rate, $S_t = S_0 e^{-rt}$, then r, the instantaneous rate of evacuation, = 0.079 h^{-1}. Mean values from all fish at each time

TABLE 1. Stomach volume and average and maximum meal sizes for winter flounder of different weights.

Fish wet wt (g)	Stomach vol. (cm^3)	Avg. meal size (cm^3) (fed once/24 h)	Max. meal (cm^3) (fed once/24 h)
19	1.4	0.4	0.8
39	1.2	0.2	1.1
50	1.1	1.1	2.3
52	2.4	1.0	1.8
56	2.6	1.6	3.7
58	2.6	1.7	2.6
81	3.8	0.8	3.8
102	3.4	1.6	4.6
115	5.4	3.8	6.8
122	8.0	2.7	5.5
162	7.0	0.6	2.9
165	13.0	1.0	3.6
231	12.0	3.8	8.1
350	16.0	4.6	7.9
392	12.0	5.9	9.6

TABLE 2. Average amount of food (as % initial meal) remaining in winter flounder stomachs at different time intervals after an initial meal. Treatment A involved feeding fish to satiation at the specified time intervals following the initial meal and treatment B involved killing the fish and weighing the stomach contents at the specified time intervals.

Experimental treatment	Time after initial meal (h)					
	2	4	6	12	24	55
A	77 (n=18)	68 (n=18)	48 (n=18)	40[a] (n=18)	13 (n=21)	
B	83 (n=4)	95[b] (n=4)	58 (n=3)	77[b] (n=3)	46 (n=3)	12 (n=1)

[a]This value is probably an overestimate as winter flounder are visual feeders normally eating only in the daylight (Olla et al. 1969; Klein-MacPhee 1978), and these experiments were conducted in the dim light of the "night" of the diurnal light cycle.

[b]At each of these times one of the fish dissected had >100% (120 and 115%) of the initial meal in its stomach.

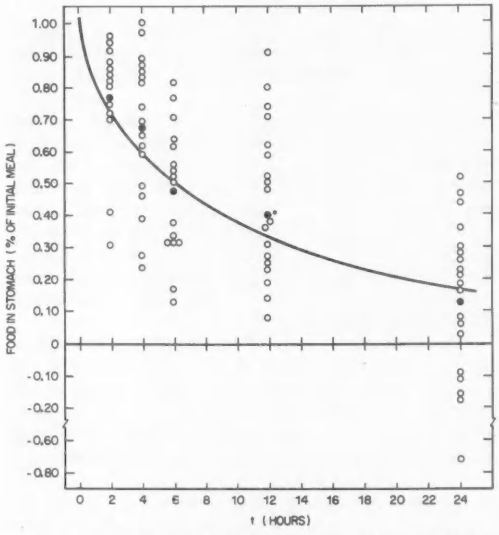

FIG. 1. Stomach content (as % initial meal) at various times (t) after initial meal estimated from voluntary food intake at time t. Each point is the average for an individual fish at time (t). Circled values are means for all fish at time t. Curve is fitted to means by eye. *Value at 12 h may be an overestimate. (See Table 2.)

were used as there was no relation between fish size and gastric evacuation expressed in this manner.

Discussion — The rate of hunger return has been successfully used to estimate gastric evacuation both in fish with stomachs (flounder, Kiørboe 1978) and in fish without stomachs (blenny, Grove and Crawford 1980). This method has several advantages over sequential sacrifice and X-ray studies. Once the fish have acclimated to laboratory conditions and are feeding voluntarily, the method is essentially non-traumatic. Evidence of this in winter flounder was their assumption of the visual search posture (Olla et al. 1969) at feeding time once they were conditioned to the procedure. This eliminates bias which can be introduced by force feeding (Windell 1966; Swenson and Smith 1973), or repeated handling involved in X-ray or stomach-pumping procedures (Fänge and Grove 1979). In addition, experiments can be repeated with individual fish permitting estimation of intra- and inter-fish variability. Furthermore, unlike X-ray techniques, the results provide a continuous quantitative measure of evacuation rate rather than simply the time to empty the stomach completely.

The assumption behind estimation of evacuation rate from hunger recovery is that the amount of food voluntarily consumed by a fish is equal to the portion of the preceding meal already digested. Available evidence (reviewed by Vahl 1979) supports this assumption. After fish are fed to satiation, hunger recovery, in some species (e.g. brown trout (*Salmo trutta*), Elliott 1975a, b; sockeye salmon (*Oncorhynchus nerka*), Brett 1971), initially lags slightly behind gastric evacuation. Hunger recovery in other species such as O-group flounder (Kiørboe 1978) and rainbow trout (*S. gairdneri*) (Grove et al. 1978) does not show a comparable delay. Dissecting a small number of fish at known intervals following a short period of voluntary feeding gives a direct comparison of stomach fullness and hunger recovery. For example, dissections indicated that at the temperatures used, complete evacuation of a meal takes longer than 24 h (probably between 48 and 72 h) which agrees reasonably well with the estimate of 57 h for 99% evacuation determined by calculations from the rate of hunger recovery. Because the goal of many studies is to predict daily consumption by fish in the field, the rate of hunger return is probably more meaningful than actual stomach fullness.

Hunger is a response to a complex of factors especially stomach fullness, food type, and nutrient levels in the blood (Vahl 1979; Jobling 1980). The presence of food from a previous meal in the stomach, and presumably elevated nutrient levels in the blood under conditions of ample food availability, may contribute to the variable feeding pattern (see also Kiørboe 1978; Grove and Crawford 1980) observed in the laboratory. Similar variability in daily consumption may occur in the field in response to changes in quantity and type

of prey available (Jobling 1980). Sockeye salmon (Brett 1971), brown trout (Elliott 1975a), dab (Grove et al. 1978), and turbot (Flowerdew and Grove 1979) all increase consumption per meal when deprived of food for increasing periods of time. Thus, a fish in the field might consume an unusually large meal after several days of relatively poor foraging. This would be anatomically possible, especially for winter flounder >100 g, as comparison of stomach volume with mean meal size indicated that in the presence of surplus food, these fish usually do not completely fill their stomachs (Table 1). This suggests that methods of calculating daily ration based on maximum stomach fullness of field-caught specimens probably overestimate daily consumption; mean stomach content is likely to be a more realistic parameter (Jones 1978).

As in many other fish recently studied, evacuation rate is exponential (Brett and Higgs 1970; Elliott 1972; Tyler 1977; Persson 1979; Grove and Crawford 1980) and, like consumption (Swenson and Smith 1973; Grove et al. 1978), is independent of fish size. The value of r we obtained, 0.079, agrees well with the values found by Kiørboe (1978) for O-group flounder (*Platichthys*) feeding on polychaetes in the laboratory.

Calculations of daily ration based on preliminary data for a late autumn population (mean length 50.5 cm) from Georges Bank resulted in estimates of daily consumption for winter flounder of 1.3–1.5% body weight per day (Huebner et al. unpublished data) using three independent models for calculating daily ration (Elliott and Persson 1978; Eggers 1979; Lane et al. 1979). These calculated values are in close agreement with daily consumption by winter flounder feeding ad lib in the laboratory at similar temperatures (1.8–2.4% this study; 2% Tyler and Dunn 1976). The somewhat higher values from laboratory studies are likely due to the smaller average size of fish used in these studies.

Our estimates of evacuation rate allow us to approximate food requirement (daily ration) of winter flounder feeding on the soft-bodied prey which constitute >50% of their diet (Langton and Bowman 1982). These values may not be valid when the diet consists of crustaceans, echinoderms, and other organisms with exoskeletons or hard parts. If food is diluted with undigestable materials (e.g. Kaolin, $BaSO_4$), consumption and evacuation rates increase to compensate for the decrease in caloric content (Rozin and Mayer 1961, 1964; Lee and Putnam 1973; Grove et al. 1978; Jobling 1980). Fish in the field are likely to show a similar response when feeding on low-calorie food sources. Changes in consumption, digestion, and differential retention of materials in the stomach need to be examined further using prey items representative of the fishes' natural diet. This would provide, in addition to specific estimates of daily consumption, a quantitative description of predation pressure exerted by a predator on its prey. Thus, further laboratory determinations of gastric evacuation rates for different temperatures and prey, combined with adequate field data, are necessary for the development of reliable and comprehensive multispecies assessment models.

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Stream Regulation Alters Acute Temperature Preferenda of Red Shiners, *Notropis lutrensis*

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Acute selected temperatures at acclimation states of 10, 20, and 30°C were significantly different ($P < 0.05$) between red shiners (*Notropis lutrensis*) from an unregulated stream and a stream below a hypolimnion-release reservoir in north central Texas. Estimated final temperature preferenda for the two populations were 30.0 and 23.3°C, respectively. These results support the hypothesis that temperature selection behavior in this species is mutable and subject to regulation by natural selection. We hypothesize that the lower thermal preferendum of tailwater populations represents an adaptive response to a depressed thermal regime typical of hypolimnion-release reservoirs.

Key words: temperature preferendum, regulated stream, red shiner, *Notropis lutrensis*

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Les températures préférées aiguës de sujets acclimatés à 10, 20 et 30°C diffèrent de façon marquée ($P < 0,05$) chez des ménés rouges (*Notropis lutrensis*) d'un cours d'eau non régularisé et d'un cours d'eau en aval d'un réservoir de vidange de l'hypolimnion dans le centre-nord du Texas. Les températures préférées finales estimées chez les deux populations sont de 30,0 et 23,3°C respectivement. Ces résultats appuient l'hypothèse que le choix de la température par cette espèce est variable et réglable par sélection naturelle. Nous avançons l'hypothèse qu'une température préférée plus basse chez les populations du cours d'eau d'aval sont une réponse adaptive à un régime de basse température typique des réservoirs de vidange de l'hypolimnion.

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RECENT data suggest that variability in reported final preferenda of fish, previously regarded as species-specific (Goddard and Tait 1976; Coutant 1977; McCauley 1977), may represent adaptive responses of allopatric populations to environmental variability (Hall et al. 1978). If the final temperature preferendum of a fish is regulated strongly by natural selection (See Beitinger and Fitzpatrick 1979), variation in behavioral responses to temperature should then accompany changes in temperature-modulated physiological and biochemical selective pressures. Hampered by statistical interpretation (see Mathur and Silver 1980) and the lack of technique standardization (Gift 1977), little definitive evidence has been offered to support such mutability in temperature selection behavior. Clearly, research is needed to determine if intraspecific variation in thermoregulatory behavior exists and is an adaptive response of fishes to thermal differences among aquatic ecosystems.

Research was designed to determine the temperature preference of populations of a cyprinid, the red shiner (*Notropis lutrensis*), collected from regulated and natural lotic environments of the Brazos River in north central Texas. The regulated portion of the river has been influenced by hypolimnetic release associated with a hydroelectric facility since the completion of Morris Sheppard Dam and Possum Kingdom Reservoir in 1941. This results in a depressed thermal regime in tailwaters of the reservoir and creates a summer-cool, winter-warm river with numerous riffles typical of spring-fed streams of the north, but atypical of rivers of north central Texas (Cloud and Stewart 1974). Red shiner populations within 57 river kilometres downstream of the impoundment have undergone significant genetic change at the malate dehydrogenase-B (MDH-B) locus, relative to other local populations (Richmond and Zimmerman 1978; Zimmerman and Richmond 1981). These investigators have observed changes in zygotic frequencies and an increase in heterozygosity at this locus associated with a rapidly fluctuating thermal regime during peak period power generation, similar to genetic variation in mummichog (*Fundulus heteroclitus*) populations under the influence of a heated effluent from a power plant (Mitton and Koehn 1975).

We hypothesized that concomitant with the alteration of zygotic frequencies of this key metabolic enzyme, differences in temperatures selected by the red shiner from regulated and unregulated portions of the river should exist; therefore, we determined the acute preferred temperatures (Reynolds and Casterlin 1979) of red shiners from these two populations to test our hypothesis.

Materials and methods — Red shiners (29–47 mm, $\bar{x}$ = 35.0 mm SL) were collected between November 1979 and February 1980 from the Brazos River, 30 km downstream from Morris Sheppard Dam (Palo Pinto County, Texas) and the Clear Fork of the Brazos River (17.7 km SW Graham, Young County, Texas) above the reservoir. Water temperatures at both locations ranged from 15 to 18°C in November, to 7°C in February.

Fish were held initially at capture temperature for 5 d in aerated and filtered 38-L aquaria. Aquarium water temperatures were maintained (±0.5°C) by submergence in a cooling water bath equipped with circulating thermoregulators. Photoperiod of LD 15:9 was maintained during acclimation and experimentation. Fish from each site were acclimated to 10, 20 and 30°C at a rate of 1.0° per day, and once at their respective acclimation temperatures, were held there for 7 d prior to testing. All fish were fed trout chow ad libitum according to the following schedule: every 3rd day at temperatures of 10°C or less, on alternate days between 10 and 20°C, and daily between 20 and 30°C. One regular feeding was withheld prior to testing.

Acute temperature selection trials were conducted in an epoxy-painted sheet metal trough (305 × 31 × 31 cm), modified from Cherry et al. (1975). Alternately arranged transverse baffles divided the trough into ten 30.5-cm cells, each with a 9.5-cm access to adjacent cells. Dechlorinated water, introduced at one end from a circulating cooling bath, was warmed as it passed through the trough by a battery of rheostatically controlled, 250-W lamps positioned under the trough. The temperature of each cell was monitored (±0.1°C) by a centrally positioned thermistor. Water depth was maintained at 5 cm to prevent vertical temperature stratification.

All trials were conducted between 10:00 and 16:00 and initiated by introducing three fish from a population to the gradient at a point corresponding to their acclimation temperature. Following a 20-min orientation period, fish positions were monitored at 2-min intervals for 40 min. Tests were replicated for each population and acclimation temperature. The median of data pooled from replicate tests was taken as the acute selected temperature by each population at each acclimation temperature, as recommended by Richards et al. (1977).

A two-way analysis of variance (ANOVA; Sokal and Rohlf 1969) was used to test for differences in temperature selection between acclimation temperatures and capture location. The final temperature preferendum of each population was estimated from a graph of acclimation temperature vs. selected temperature following Fry (1947).

Results and discussion — Red shiners from both locations acclimated to 10 and 20°C selected temperatures higher than acclimation temperatures; at 30°C acclimation, red shiners from the regulated portion of the Brazos River selected 28.5°C, while the unimpacted Clear Fork population selected 30.0°C. The greatest difference in selection responses of the two populations occurred at 20°C acclimation, where Brazos fish selected 22.3°C, and Clear Fork fish selected 27.8°C (Table 1). Significant differences existed in the temperatures selected by fish acclimated to different temperatures and between Brazos and Clear Fork populations of red shiners (two-way ANOVA $P < 0.05$).

The final temperature preferendum, defined as the point where selected and acclimation temperatures are equal, represents the temperature towards which fish will gravitate when released from the confines of previous thermal history and exposed to an expanded gradient (Fry 1947, 1964). Variation in final temperature preferenda among populations of a species (i.e. temperature selection ecotypes) represent adaptive responses to different environmental selective pressures. From acute temperature selection vs. acclimation plots, we estimate the final temperature preferendum for each population as 30.0 and 23.3°C for red shiners from the Clear Fork and the regulated section of the Brazos River, respectively (Table 1).

TABLE 1. Median acute selected temperature (°C) for two populations of *Notropis lutrensis* following acclimation to 10, 20, and 30°C. Median observations and interquartile ranges are from ranked observations, pooled from replicate tests. Final preferenda were estimated visually from intercept technique (Fry 1947).

	Clear Fork population acclimation temp. (°C)			Regulated Brazos population acclimation temp. (°C)		
Observation	10	20	30	10	20	30
Median	23.0	27.8	30.9	21.2	22.3	28.5
Interquartile ranges	20.8–24.2	25.7–29.7	25.8–33.5	15.6–23.7	17.8–26.4	24.9–32.6
Final preferendum		30.0			23.3	

Available data on the temperature preferenda of cyprinids (see Coutant 1977) indicate a diversity of responses among members of the genus *Notropis*, which probably correlates with their wide distribution. The lower value estimated for our Brazos population, inhabiting the tailwaters of a hypolimnetic-discharge dam, supports our test hypothesis and the contentions of Matthews and Hill (1977; 1979) that the species is adaptable to wide thermal variation. Brazos red shiners exposed to hypolimnetic discharges apparently have achieved a depressed final preferendum. This strategy is clearly adaptive, for hypolimnetic-discharge regulation creates a decreased amplitude in ambient water temperature variation (i.e. summer-cool, winter-warm) and an overall depressed thermal regime (Stanford and Ward 1979). Such differences have been documented for the sites sampled in this study (Cloud and Stewart 1974; Zimmerman and Richmond 1981).

In a companion study, the acute thermal preferenda of two populations of a closely allied species, the blacktail shiner (*N. venustus*), were determined (Calhoun et al. 1981). Again, a population from the regulated portion of the Brazos River was compared to a population from a natural system in a nearby river, the Trinity. Both populations of *N. venustus* demonstrated similar responses to the thermal gradient, and the acute thermal preferenda were not significantly different. The acute temperature preferences of *N. venustus* were similar to those of impacted *N. lutrensis* over similar temperature acclimation ranges. The lotic habitat of the blacktail shiner in Oklahoma and Texas is typified by cool, clear, gravel-bottom streams (Miller and Robison 1973), typical of regulated portions of the Brazos River (Cloud and Stewart 1974; Zimmerman and Richmond 1981). The environmental buffer, provided by stream regulation, seems to have elicited from red shiners a behavioral response converging upon that of the blacktail shiner, whose distribution is restricted to cooler, more thermally static habitats (Miller and Robison 1973).

This research supports the hypothesis that the final temperature preferendum of a fish species is a mutable response subject to regulation by natural selection. If the final preferendum coincides with optimum temperatures for key metabolic and physiological processes (Beitinger and Fitzpatrick 1979), then whole-animal responses should differ concomitantly with temperature selection behavior. Similarly, if temperature selection behavior is under genetic control, we should expect to see parallel changes in gene-regulated metabolic pathways suggestive of a selective advantage. Indeed, the associated increase in the proportion of heterozygotes at the MDH-B locus in red shiners from regulated sections of the Brazos River and the relationship of this enzyme to the thermal response of fish (Zimmerman and Richmond 1981) appears to substantiate these parallel changes. More comprehensive studies need to be performed on a site-specific basis and to involve assay techniques performed at and about the final temperature preferendum to elucidate the adaptive significance of the final preferendum of fish.

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LETTERS AND COMMENTS/LETTRES ET COMMENTAIRES

Comment on the Role of Fishes in the Regulation of Phosphorus Availability in Lakes

COMMENT

In 1975 Lamarra demonstrated that the digestive activities of carp, a benthivorous fish, release considerable amounts of phosphorus into the overlying water. He further demonstrated that such releases, which result in increased algal biomass, can be important contributors to the nutrient budgets of lakes.

In their recent paper, "The Role of Fishes in the Regulation of Phosphorus Availability in Lakes" (Can. J. Fish. Aquat. Sci. 37: 1540–1549), Nakashima and Leggett reject Lamarra's hypothesis and conclude that fish have a minor role in the recycling of phosphorus. We think that these authors have misunderstood the meaning of their own work relative to that of Lamarra, and in doing so, have incorrectly concluded that the role of fish is unimportant.

Nakashima and Leggett base their conclusions on a comparison of phosphorus excretion by fish to the total phosphorus uptake by seston. Compared to sestonic uptake, phosphorus release by fish is certainly negligible, but the comparison is irrelevant to the hypothesis posed by Lamarra. Lamarra's hypothesis deals with the possibility of a fish-mediated increase in the loading of phosphorus to the open waters of lakes. This increased loading, coupled with the well-known chlorophyll/phosphorus relationships demonstrated by many investigators (e.g. Dillon and Rigler 1974; Smith and Shapiro 1981), leads to the expectation that systems with abundant benthivorous fish will have higher mean standing crops of algae than would be expected from knowledge of the external nutrient loading of the lake.

Nakashima and Leggett have confused the issue by equating Lamarra's studies of a benthivorous fish, carp, with excretion rates of planktivorous zooplankton and perch (a fish which may be piscivorous, planktivorous, and/or benthivorous). Excretion of phosphorus by such planktivorous organisms cannot increase the total amount of phosphorus in the open water because they are themselves part of the open water system. Addressing this very problem in regard to zooplankton, Peters and Rigler (1973) stated, "... it may be more useful to enquire into the efficiency with which zooplankton cycle P than to ask if regeneration of P by zooplankton is adequate to meet the photosynthetic requirements of phytoplankton."

On the other hand, benthivorous fish such as carp, bullheads, and even perch, to the extent that they feed on benthic invertebrates, are not within the open water food chain and therefore can, through excretion, increase total phosphorus of the open water.

The importance of phosphorus excretion by these fish to the open water phosphorus budget is best gauged by comparison of the phosphorus excreted with the external loading of the lake. Thus, in L. Memphremagog, the excretion by the fish of a "negligible" 0.11–0.33% of the total uptake of P by the seston would have added 2148–6445 kg P to the open water between June 1 and September 30, if the fish had been, as in Lamarra's studies, exclusively benthivorous. This contribution is not insubstantial, considering that the June–September external loading to the same south basin of Lake Memphremagog was only slightly in excess of 3550 kg P (Carlson et al. 1979). Certainly the impact of this comparison is tempered by the mixed feeding roles of the Memphremagog fishes and by the use by Nakashima and Leggett of total phosphorus rather than orthophosphorus in the excretion estimates, but the comparison indicates that the potential importance of phosphorus excretion by the fish of Lake Memphremagog is entirely consistent with Lamarra's findings.

Nakashima and Leggett close their paper with the comment, "By demonstrating the minor importance of phosphorus excretion by fishes to the phosphorus dynamics of lakes, we hope to redirect future research towards an examination of alternative hypotheses ... which appear to merit further study." We think Nakashima and Leggett have confused rather than clarified the issue, and we would certainly not reject the importance of bottom-feeding fish on the basis of their data and go galloping off in other directions. — JOSEPH SHAPIRO, *University of Minnesota, Minneapolis, MN 55455, USA* AND ROBERT CARLSON, *Kent State University, Kent, OH, USA*.

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How important is phosphorus excretion by fish to the phosphorus dynamics of lakes?

REPLY

Shapiro and Carlson (1982) have charged that (1) we (Nakashima and Leggett 1980) concluded fish have a minor role in the recycling of phosphorus in lakes and (2) that by failing to consider the importance of benthic-feeding fishes in

the internal P loading of lakes we misinterpreted the significance of Lamarra's (1975) work. We contend that these statements are misleading and that they result from (1) a superficial reading of our paper and (2) an uncritical acceptance of Lamarra's conclusions.

We first reject their statement that we concluded "fish have a minor role in the recycling of phosphorus." We rejected *only* the hypothesis that P excretion by fish is a major nutrient source for primary producers in lakes. The greater portion of our discussion was, in fact, devoted to a consideration of alternative hypotheses concerning ways that fish might influence rates of P recycling. As examples we considered the indirect control of P excretion rates by zooplankton through size selective predation by fish; the removal of P from the epilimnion through storage in fish tissue (nutrient sinks); and the release of stored P through decomposition at death. These hypotheses are supported by the results of several studies (e.g. Durbin et al. 1979; Henrikson et al. 1980; Kitchell et al. 1979). Hence, rather than rejecting the role of fish in P recycling in lakes we argued for its importance and attempted to focus future work on the most promising hypotheses dealing with the mechanisms of this regulation.

The second criticism that "by equating Lamarra's studies of a benthivorous fish, carp, with excretion rates of planktivorous zooplankton and perch" we "confused the issue" rests on two assumptions, both of which are tenuous. The first assumption is that Lamarra's (1975) study actually demonstrated, as he claimed, that P *excretion* by carp was a significant P source for algae. His conclusion was based on the results of two series of experiments in which carp were added to enclosures, and changes in total P were compared to changes in similar enclosures lacking carp. These experiments failed to reject systematically at least two alternative hypotheses. The first of these is that higher P levels in the enclosures containing benthivorous carp were due to disturbance of the sediments, or of the sedimented, decomposing algae, by the feeding and swimming activity of the fish (Miller et al. 1961; Hilsenhoff 1965). In this regard we are not convinced that the near-continuous disturbance of the sediments by the swimming and feeding activities of carp in the shallow (1.6 m) experimental enclosures was adequately simulated by stirring the sediments in the control enclosures "with a paddle once a week" (Lamarra 1975, p. 2462). The second hypothesis, which relates only to enclosures in which the fish were at liberty to forage on the lake bottom, is that carp caused a reduction in the average size of individuals in the benthic invertebrate community by size-selective predation (Hall et al. 1970) thereby increasing the per-unit-biomass P excretion rate by the benthos (see Ferrante 1976; Johannes 1964, 1965; Nakashima and Leggett 1980; Peters and Rigler 1973). Probable shortcomings of his experimental determinations of P excretion rates were considered in our original paper (Nakashima and Leggett 1980, p. 1544). In conclusion, the results of Lamarra's experiments do not allow any conclusions to be drawn concerning the mechanism(s) by which total P values were increased in the enclosures. The second assumption implicit in their criticism is that the rate of P excretion by a benthic community composed of invertebrates alone is less than the rate characteristic of a benthic community that includes fish. There is no evidence that this is so. P excretion per-unit-biomass is inversely proportional to body size (Ferrante 1976; Johannes 1964, 1965; Nakashima and Leggett 1980; Peters and Rigler 1973). Hence the impact of the addition of benthivorous fish on the total community P excretion rate (loading) would depend on a complex of variables including, but not exclusive to, changes in the average body size/biomass ratio resulting from the addition of fishes, changes in the average seasonal biomass of the invertebrate fauna, the dominant habitat of the resulting invertebrate community (epibenthic vs infrabenthic) etc.

We return now to the question originally asked by Lamarra (1975) and by ourselves (Nakashima and Leggett 1980), does the *excretion* of P by fish add significantly to the total open water phosphorus pool of the lake? Lamarra's experiments with carp in enclosures shed no light on the question. Our experiments with perch, which feed omnivorously on plankton, benthos, and fish (Nakashima and Leggett 1975, 1978), and thus typify the feeding activity of the diverse fish fauna characteristic of most lakes, suggest that the contribution is very small. The maximum daily loading resulting from the activity of such a fish fauna represents much less than 1% of the daily P requirements of the seston (0.11−0.33% in Lake Memphremagog). It should be stressed that this estimate *includes* the contribution from benthic-feeding fishes for which Shapiro and Carlson (1982) expressed such concern. Their assertion that P excretion by fish in Lake Memphremagog could equal the total summer external P loading to the lake and hence must be important is irrelevant. First, the total fish biomass is not exclusively benthic, nor is it likely to be in many lakes. Secondly, as external loading contributes a maximum of 0.18% of the summer total P requirements of the seston, the argument that excretion of P by fishes could equal or exceed this very minor contribution (given the unlikely scenario of a totally benthivorous fish community) is less than compelling.

In summary, we continue to assert that the supply rate of phosphorus resulting from the release of biologically bound P, whether planktonic or benthic, because of fish feeding pales in comparison with the rates of supply from excretion by the zooplankton (and the benthic invertebrate community) and with the daily requirements of the seston. — BRIAN S. NAKASHIMA, *Fisheries and Oceans, Northwest Atlantic Fisheries Center, P.O. Box 5667, St. John's, Nfld., A1C 5X1* AND WILLIAM C. LEGGETT, *Department of Biology, McGill University, 1205 Avenue Docteur Penfield, Montreal, Que. H3A 1B1.*

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Comment on Estimating the Average Age of First Birth in Marine Mammals

Recently Dr J. M. Breiwick, National Marine Fisheries Service, pointed out that in my article entitled, "Estimating the average age of first birth in marine mammals". (Can. J. Fish. Aquat. Sci., Vol. 38: 237–239), that it is more reasonable to assume that cov $(y(x), y(x)\, z(x-1))$ does not equal 0, as I assumed; and further that the more acceptable assumption produces a variance estimate that is significantly smaller than the variance estimate that I proposed. Dr Breiwick has derived an estimate of var $(\hat{z})$, which should replace equation 6 in my paper:

$$\text{var}\,(\hat{z}) = [1 - \hat{z}(x-1)]^2\, \text{var}\,\hat{y}(x) + [1 - \hat{y}(x)]^2\, \text{var}\,\hat{z}(x-1).$$

The affect of this change in estimating SE $(\bar{x})$ is significant. Using Breiwick's equation for var $(\hat{z})$, the SE $(\bar{x})$ should be 0.58, and not 6.77. I appreciate Dr Breiwick pointing this out, as the sample size needed to detect a difference of 2 years is roughly 125 animals, and not 600 animals. There is also a typographical error in Table 1. The number of females age 1 with young should be 0, not 6. — D. DEMASTER, *United States Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038, USA.*

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BOOK REVIEW/COMPTE RENDU

Fish Diseases. *Edited by W. Ahne. Springer-Verlag, New York. 1980. xi + 252 p. $49.80 U.S.*

This collection of excellent papers was initially presented in Munich, in October 1979, at the Third Session of the Cooperative Program of Research on Aquaculture (COPRAQ), Fish Disease Section Meeting. This session was organized jointly by the European Inland Fisheries Advisory Commission of the Food and Agriculture Organization of the United Nations, and the Office International des Epizooties. Unfortunately, this book is not a complete report of the actual proceedings because the two round-table discussions, on viral and bacterial diseases, have been omitted from the text.

The major research topics covered at this meeting included the study of host–pathogen interactions with emphasis on defense mechanisms, the investigation of disease transmission and mode of initiation of infection, and the creation of model systems for the study of pathogenesis under controlled conditions. Diseases that were emphasized were of particular concern in the rearing of salmonids and cyprinids. These infectious diseases included viral hemorrhagic septicemia (VHS), infectious pancreatic necrosis (IPN), vibriosis, furunculosis, spring viremia of common carp (*Cyprinus carpio*), and carp erythrodermatitis. There was further recognition of emergent problems associated with bacterial and proliferative kidney disease, as well as with other disorders, including newly recognized diseases caused by water-borne bacteria and by certain protozoa such as *Dermocystidium* and *Sphaerospora*. Two papers delineated the world-wide occurrence of chronic nephrocalcinosis in certain intensive culture operations, particularly in those facilities having sources of well water with high levels of dissolved carbon dioxide.

A major contribution, toward the understanding of viral pathogenesis in fish, was made by papers substantiating the probable role of the gills and the pillar cells in the initiation of infection by the rhabdoviruses. Further cooperative work by Meier and Jørgensen indicated that the VHS virus has a broad host range and that its pathogenicity extends to pike fry, as well as to young salmonids other than rainbow trout. Although evidence exists for limited immunocompetence in small fish, the cooperative paper by Hill, Dorson, and Dixon on IPN viral immunization verified continuing technical problems with the development of effective vaccines against the salmonid viruses. The use of avirulent or attenuated IPN virus administered by an immersion method appeared the most promising in offering protection. The possibility of reversion to virulence must be considered, however, as a major impediment to the development of a safe commercial live vaccine. Notably absent from the virology section were papers on experimental immunization with the salmonid rhabdoviruses. One anticipates that more information will soon be forthcoming on the significant function of complement in the protection of fish against the enveloped or lipid-containing viruses.

Several experimental studies with *Vibrio* and *Aeromonas* established possible roles for soluble toxins in the pathology of vibriosis and furunculosis, thus demonstrating the need to consider such factors in the development of bacterins (because antibodies to these diffusible antigens may be significant in conferring protective immunity in fish). Development of suitable challenge systems, for bacterin development, were aided by studies of host defense mechanisms and the establishment of model systems of bacterial pathogenesis. Work presented from laboratories in Britain, France, Canada, and Ireland indicated that rapid progress is being made towards the development of an effective bacterin that will be commercially available for the prevention of furunculosis. Particularly encouraging were the results presented in the cooperative paper by Smith, McCarthy, and Paterson on furunculosis immunization of brown trout (*Salmo trutta*). The fact that *Aeromonas salmonicida* is not restricted to causing furunculosis in salmonids was stressed by several other investigators, who demonstrated that *A. salmonicida* produces erythrodermatitis in carp.

Fish pathology is no longer simply a descriptive science; instead it has obviously progressed to the state where sophisticated experiments on immunology and pathobiology are yielding positive benefits in the form of new methods of disease prevention and control through vaccination and chemotherapy. This book is of particular interest to microbiologists, to graduate students, and to other specialists in fish diseases interested in keeping informed of recent research developments in fish pathology. The next publication of this series, undoubtedly, will prove to be equally significant.

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CORRECTIONS TO RECENT PUBLICATIONS
CORRECTIONS SUR RÉCENTES PUBLICATIONS

VOLUME 38, No. 2 — paper by D. R. Bernard: *Multivariate analysis as a means of comparing growth in fish.*

PAGE 234: Equations (6) and (7) should read

$$(6) \quad (p_{1j} - p_{2j}) \pm \sqrt{\left(\frac{N_1+N_2}{N_1N_2}\right) s_{ij}\, T_0^2}$$

$$(7) \quad F_0 = \frac{N_1N_2\,(N_1+N_2-4)\,(p_{1j} - p_{2j})^2}{3(N_1+N_2)\,(N_1+N_2-2)s_{ij}}$$

VOLUME 38, No. 4 — paper by A. H. Berst, A. R. Emery, and G. R. Spangler: *Reproductive behavior of hybrid charr (Salvelinus fontinalis × S. namaycush).* In this paper the spelling of the word charr differs from that (char) used in *A List of Common and Scientific Names from the United States and Canada*, by the American Fisheries Society, and is preferred by the authors.

VOLUME 38, No. 5 — paper by D. M. Rosenberg and V. H. Resh et al.: *Recent trends in environmental impact assessment.*

PAGE 595: Right column, line 26, "Quantitive" should read "Quantitative."

PAGE 596: Heading over right-hand column should be "Matrices — general."

PAGE 613: Figure 5, Fossil Fuels, colony development histogram should read "(U.S.D.I.B.L.M. 1977b)."

PAGE 620: Craig et al. 1979, "J. Environ. Manage." should be "Environ. manage."

VOLUME 38, No. 6 — paper by W. Van Winkle, D. S. Vaughan, L. W. Barnthouse, and B. L. Kirk: *An analysis of the ability to detect reductions in year-class strength of the Hudson River white perch (Morone americana) population.*

PAGE 629: Between equations (8) and (9), the second sentence should read "Using s_1^2 as an estimate of s_p^2."

PAGES 630 and 631: Figures 1 and 2 should be reversed.

VOLUME 38, No. 7 — paper by D. E. McAllister, M. E. Anderson, and J. G. Hunter: *Deep-water eelpouts, Zoarcidae, from Arctic Canada and Alaska.*

PAGE 822: Key couplet 4, "short-tailed *Lycodes*" should lead to couplet 9, not 8.

PAGE 827: Right column under Distribution, line 3, "Johsson (1960)" should read "Jonsson (1969)."

PAGE 831: Right column under Material Examined, line 8 should read "56°43′W, in 250–260 m, 4.31°C."

PAGE 835: Right column, last paragraph, line 2, "*G. viridus*" should be "*G. viridis*."

PAGE 836: Left column under Diagnosis, line 2 should read "Differs from *G. viridis* . . ."

PAGE 836: Right column, line 10, should read "triangular, short . . . pupil diameter."

PAGE 837: Right column under Description, line 8 should read "GR 2 − 4 + 9 − 12 = 13 − 15 [6]"

VOLUME 38, No. 8 — paper by M. D. Morgan: *Abundance, life history, and growth of introduced populations of the opossum shrimp (Mysis relicta) in subalpine California lakes.*

PAGE 992: Figure 2, bar over fourth histogram from right under October 31, 1977 should be omitted.

VOLUME 38, No. 10

OUTSIDE BACK COVER: Third line under Notes, "J. G. Eagles" should be "J. G. Eales." Second line under Letters and comments should read "Reply R. McKelvey and D. Hankin."

COMING NEXT MONTH / À PARAÎTRE LE MOIS PROCHAIN

Ecological studies of Arctic cod (*Boreogadus saida*) in Beaufort Sea coastal waters, Alaska
P. C. Craig, W. B. Griffiths, L. Haldorson, and H. McElderry

Food, feeding habits, and estimates of daily ration of the shortfin mako (*Isurus oxyrinchus*) in the northwest Atlantic **C. E. Stillwell and N. E. Kohler**

Bioconcentration of a hexachlorobiphenyl in Great Lakes planktonic algae
T. C. Lederman and G.-Y. Rhee

Influence of a hexachlorobiphenyl in Great Lakes phytoplankton in continuous culture
T. C. Lederman and G.-Y. Rhee

Estimating the energy budgets of actively predatory fishes **S. R. Kerr**

Limited entry policy and the Bristol Bay, Alaska salmon fishermen **J. A. Koslow**

Influence of time and size at release of juvenile coho salmon (*Oncorhynchus kisutch*) on returns at maturity **H. T. Bilton, D. F. Alderdice, and J. T. Schnute**

Growth patterns in a Newfoundland Atlantic herring (*Clupea harengus harengus*) stock
J. A. Moores and G. H. Winters

Optimal utilization of a variable fish supply **W. Silvert**

A methodology for estimating area fished for baited hooks and traps along a ground line
D. M. Eggers, N. A. Rickard, D. G. Chapman, and R. R. Whitney

Planktivorous feeding ecology of Arctic grayling (*Thymallus arcticus*)
D. Schmidt and W. J. O'Brien

Factors influencing orthophosphate turnover times: a comparison of Canadian and New Zealand lakes **E. White, G. Payne, S. Pickmere, and F. R. Pick**

Spawning and feeding behavior of captive Pacific herring, *Clupea harengus pallasi*
N. E. Stacey and A. S. Hourston

Structure–toxicity relationship of tin compounds on algae
P. T. S. Wong, Y. K. Chau, O. Kramar, and G. A. Bengert

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Application of X-ray microanalysis for the detection of heavy metals in Great Lakes algae
T. Bistricki and M. Munawar

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Influence of age, size, and temperature on metamorphosis in the starry flounder, *Platichthys stellatus* **D. Policansky**

Application of time–series intervention analysis to fish ventilatory response data
K. W. Thompson, M. L. Deaton, R. V. Foutz, J. Cairns Jr., and A. C. Hendricks

Predation of sea scallops (*Placopecten magellanicus*) by lobsters (*Homarus americanus*) and rock crabs (*Cancer irroratus*) in underwater cage enclosures
G. S. Jamieson, H. Stone, and M. Etter

An improved chamber for in situ measurement of primary productivity by sea ice algae
G. C. Schrader, R. Horner, and G. F. Smith

Graphical model of thermoregulatory behavior by fishes with a new measure of eurythermality **J. D. Giattina and R. R. Garton**

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Letters and comments/Lettres et commentaires: Comment on the role of fishes in the regulation of phosphorus availability in lakes **J. Shapiro and R. Carlson**; How important is phosphorus excretion by fish to the phosphorus dynamics of lakes? Reply **B. S. Nakashima and W. C. Leggett**; Comment on estimating the average age of first birth in marine mammals **D. DeMaster** 364–366
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